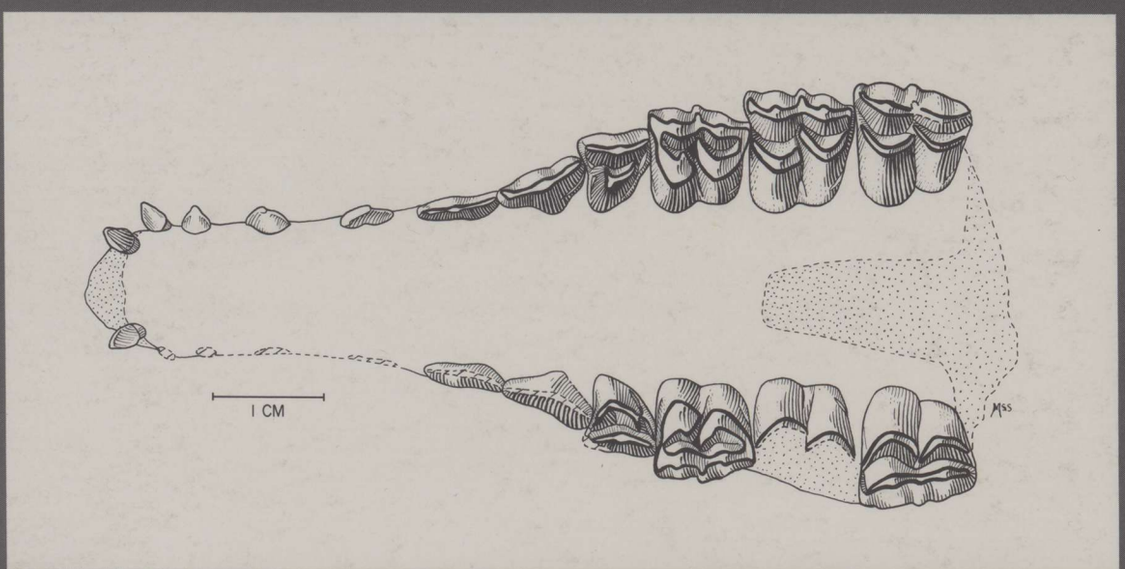
BULLETIN 23

TEXAS MEMORIAL MUSEUM

EARLY TERTIARY VERTEBRATE FAUNAS,
VIEJA GROUP AND BUCK HILL GROUP, TRANS-PECOS TEXAS:
PROTOCERATIDAE, CAMELIDAE, HYPERTRAGULIDAE

By John Andrew Wilson



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BULLETIN

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OF THE TEXAS MEMORIAL MUSEUM

EARLY TERTIARY VERTEBRATE FAUNAS, VIEJA GROUP AND BUCK HILL GROUP, TRANS-PECOS TEXAS: PROTOCERATIDAE, CAMELIDAE, HYPERTRAGULIDAE

by

John Andrew Wilson

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CONTENTS

TABLES

ILLUSTRATIONS

EARLY TERTIARY VERTEBRATE FAUNAS, VIEJA GROUP AND BUCK HILL GROUP, TRANS-PECOS TEXAS: PROTOCERATIDAE, CAMELIDAE, HYPERTRAGULIDAE

by John Andrew Wilson*

ABSTRACT

Upper and lower dentitions of *Leptoreodon marshi* from the late Eocene are described. *Leptoreodon* is placed in the Protoceratidae and the family Leptomerycidae abandoned. A new genus of late Eocene protoceratid is described and believed to be ancestral to *Heteromeryx.* An associated upper and lower dentition of *Heteromeryx* is described for the first time. *Pseudoprotoceras* is synonymized with *Poabromylus* and a new species described. *Oromeryx* and *Eotylopus* are identified from the Chadronian. A new and primitive species of *Poebrotherium* shows closer relationship to *Protylopus* than *Poebrodon.* A new genus of camelid in the Chadronian thought to be related to *Poebrodon* is described. A new species of *Leptomeryx* is described and *Leptomeryx* is placed in the Hypertragulidae. *Hypisodus* is reported from west Texas for the first time. Full selenodonty in the upper molars appears earliest in the Protoceratidae and in a family of camelids which includes *Poebrodon.* Full selenodonty in *Poebrotherium* and *Leptomeryx* is not achieved until the late Chadronian.

INTRODUCTION

The artiodactyls of the very late Uintan (including Randlett and Halfway) and the very early Chadronian (including Lapoint) other than *Agriochoerus* and *Protoreodon* are rare, poorly known, or both. Often the type consists of either an upper or a lower jaw fragment and all too often the teeth are badly worn. Additional material from the Sierra Vieja area of west Texas and the Chadron Formation of South Dakota has brought to light a few associated upper and lower dentitions from which new information can be drawn. Other forms, for example *Poebrotherium,* can now be extended back to the early Chadronian, and *Oromeryx* is now known to survive from the Uintan to the Chadronian. A new line of camelids evolved parallel with *Poebrotherium.* In addition, the presence of these forms in west Texas is recorded for the first time.

PREVIOUS WORK

This is the eighth of a series of papers relating to the stratigraphy and vertebrate faunas of the Vieja Group. They are: Wilson (1966), Hofer and Wilson (1967), Harris (1967b), Wilson *et al.* (1968), Harris and Wood (1969), Wilson (1971a; 1971b), and Wood (1973; 1974). This publication is a contribution of the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

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LOCATION AND STRATIGRAPHY

Earlier publications, primarily Stovall (1948), DeFord (1958), Wilson *et al.* (1968), and Wilson (1972) discuss the location, previous work, stratigraphy, and age of the Vieja Group (figs. 1, 2).

Wilson (1972) described a new Eocene locality in the lower part of the Pruett Formation on the Agua Fria Quadrangle (figs. 1, 2). The fauna, as yet undescribed, contains primates, rodents (Wood 1973; 1974), a large amynodont, titanothere, *Orohippus* or *Epihippus, Protoreodon,* and *Leptoreodon.* Wilson (1972) and Wood (1973) refer to this assemblage as the Whistler Squat local fauna (fig. 2). Its age, on the basis of the rodents, is believed by Wood to be Bridgerian. The presence of *Leptoreodon* and the large amynodont leads Wilson to believe that the Whistler Squat local fauna is early Uintan. This problem remains to be solved, and its solution may depend on further refinement of careful stratigraphic collecting in the type areas in Wyoming and Utah.

Descriptions of the *Leptoreodon* material from the Whistler Squat local fauna is included here. The stratigraphy of the Buck Hill Group is given in Goldich and Elms (1949), Moon (1953), and Erickson (1953). Regional stratigraphic relationships of the southern part of the Big Bend area are in McKnight (1970) and Wilson (1972).

ACKNOWLEDGMENTS

National Science Foundation grants G13270 and GP1050, the Geology Foundation, the Owen-Coates Fund of the Geology Foundation, and the University Research Institute of The University of Texas at Austin have supported the field work, the laboratory preparation, and in part, the cost of publication.

I acknowledge and thank for courtesies at their respective institutions or for providing casts or loans: Dr. Malcolm C. McKenna, Mr. Morris F. Skinner, and Mr. Beryl E. Taylor of the American Museum of Natural History, New York; Dr. Donald E. Savage, University of California, Berkeley; Dr. Mary R. Dawson, Carnegie Museum; Dr. William

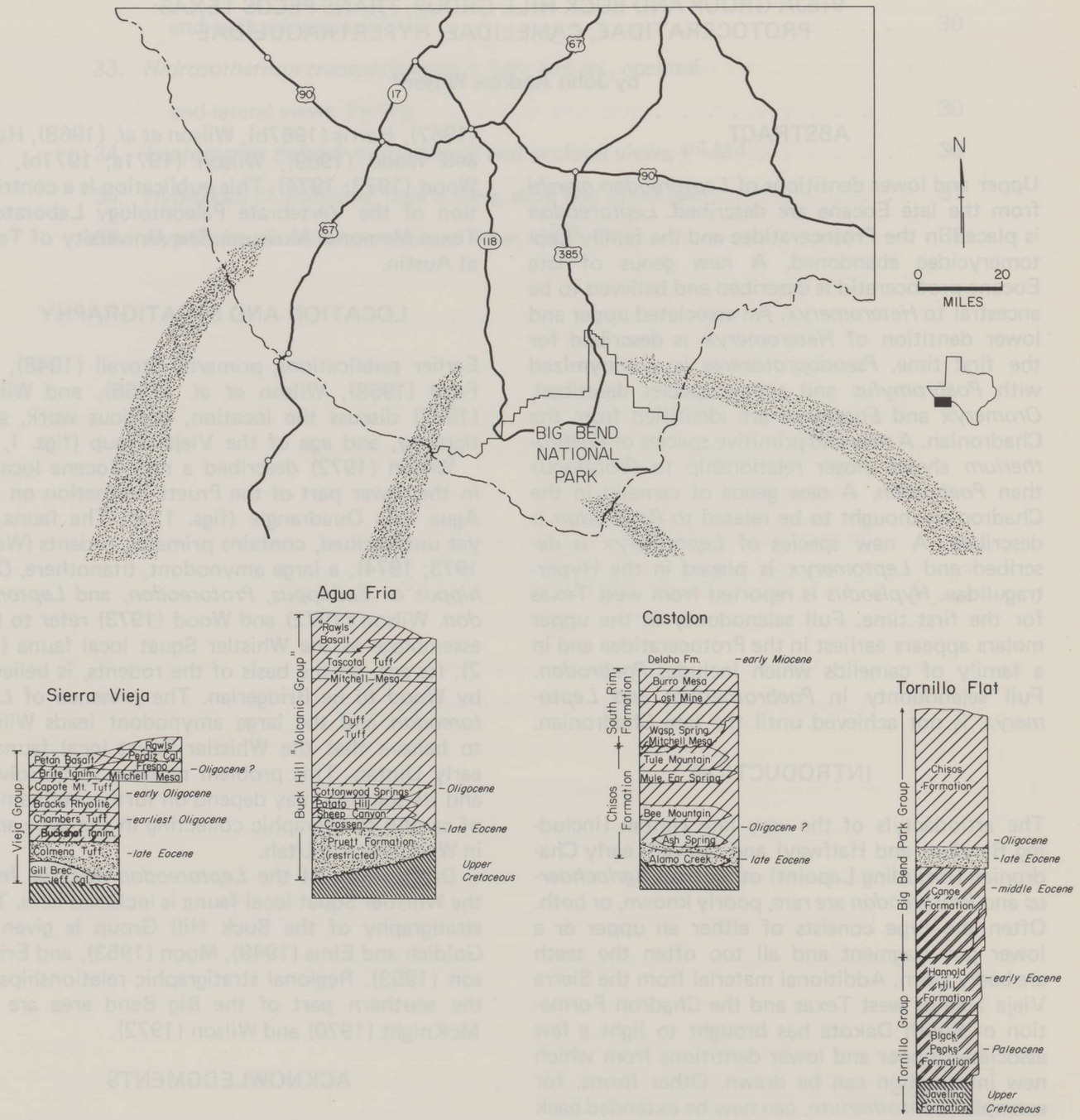


Figure 1.—Geographic location of Vieja Group and Buck Hill Group in west Texas and their approximate ages.

D. Turnbull and Dr. John Clark, Field Museum of Natural History; Dr. Theodore E. Downs, Los Angeles County Museum; Dr. David B. Kitts, University of Oklahoma; Dr. Glen L. Jepsen, Princeton University; Dr. Robert W. Wilson, South Dakota School of Mines and Technology; Dr. C. Lewis Gazin, United States National Museum; Dr. Paul O. McGrew, University of Wyoming. Dr. John Clark placed his large collection of Chadronian artiodactyls from Nebraska and South Dakota at my disposal. It proved to be an enormous help and I am grateful.

Dr. Ernest L. Lundelius was especially helpful during many conversations. I appreciate the help of Dr. James B. Stevens in working out the stratigraphy of the Agua Fria Quadrangle. Mrs. Margaret S. Stevens aided in the field work and skillfully prepared the line drawings. Mr. R. M. Frank was a most valued field assistant and laboratory technician for five years. Mr. Bill Gibson and Mrs.

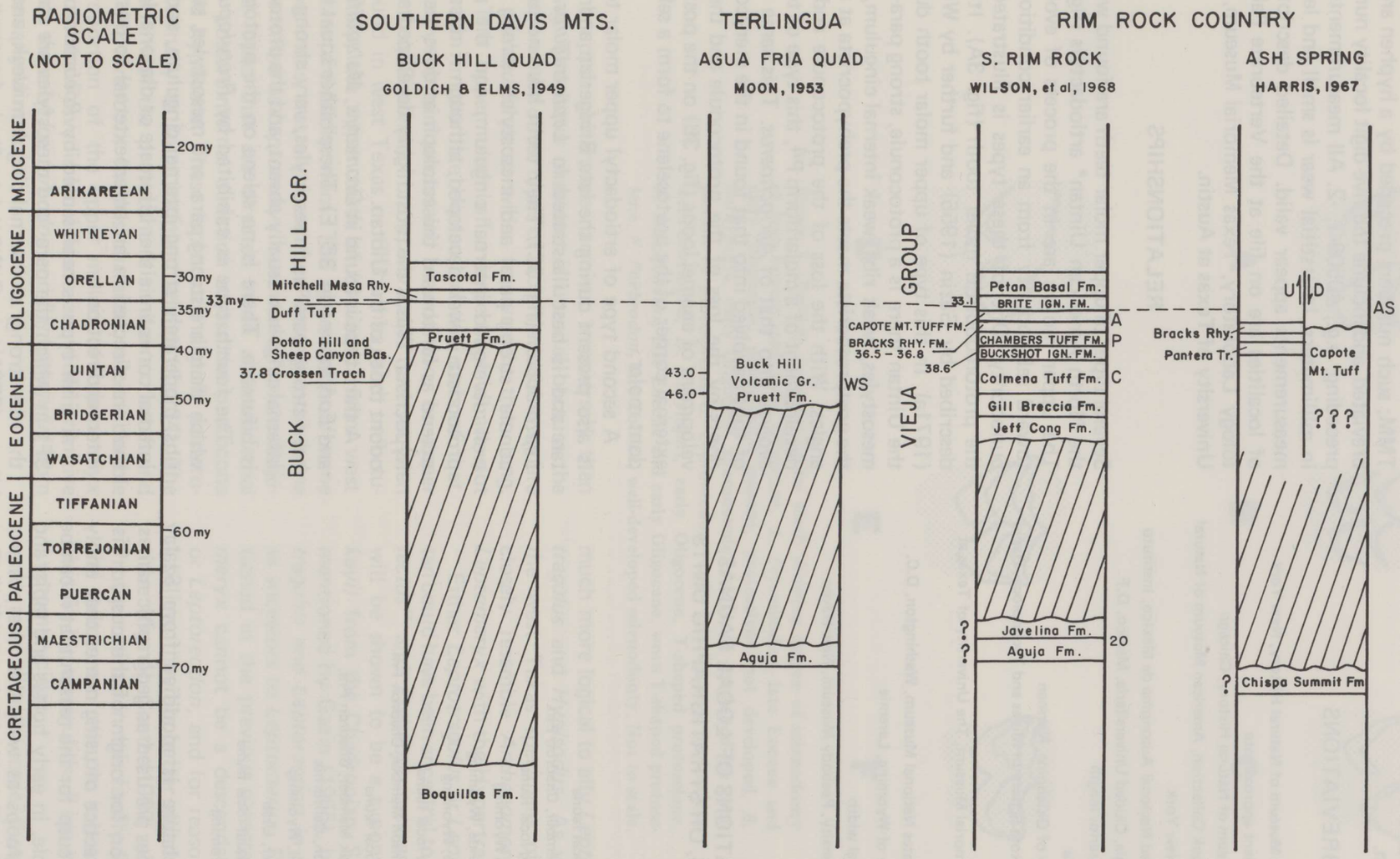


Figure 2.—Stratigraphic units in Buck Hill Group and Vieja Group with position of local faunas (see abbreviations, p. 4) and potassium-argon dates. Biotite in the bone-bearing tuff containing the Whistler Squat l.f. has been dated at the Department of Geological Sciences, The University of Texas at Austin, as 46.2 m.y.

Howard Gibson generously shared their knowledge of the geography of the area and donated their scientifically valuable collection to The University of Texas at Austin.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York
@	measurement approximate
FMNH PM	Field Museum of Natural History, Chicago
HC	Harold Cook Collection, American Museum of Natural History, New York
IGM	Universidad Nacional Autonoma de Mexico, Instituto de Geologia, Ciudad Universitaria, Mexico, D.F.
L	anteroposterior length
l.f.	local fauna
OU	University of Oklahoma, Norman
SDSM	South Dakota School of Mines and Technology, Rapid City
TMM	Texas Memorial Museum, The University of Texas at Austin
USNM	United States National Museum, Washington, D.C.
UWYO	University of Wyoming, Laramie
W	labiolingual width
YPM	Yale University, Peabody Museum, New Haven

ABBREVIATIONS OF LOCAL FAUNAS, LOCALITIES, OR STRATIGRAPHIC UNITS

A	Airstrip local fauna
Ah	Ahearn Member, Chadron Fm.
AS	Ash Spring local fauna
B	Badwater, Wyoming
BD	Beaver Divide, Wyoming
BH	Bates Hole, Wyoming
C	Candelaria local fauna
CJ	Crazy Johnson Member, Chadron Fm.
P	Porvenir local fauna
PP	Peanut Peak Member, Chadron Fm.
TR	Tapo Ranch, California
TT	Tepee Trail, Wyoming
WRU	White River, Utah
WS	Whistler Squat local fauna
Y	Yoder, Wyoming

Tooth nomenclature is modified from Szalay (1969). Cusp names are used as geographic names, with no implication for origin of the cusp. I disagree with the practice of using names that imply derivation of the cusp for the reason that it can be shown, for example, in early horses and tapirs and probably other groups as well, that the postero-internal cusp arises in a different way on adjacent teeth in the same jaw. It is inconvenient, to say the least, to carry that system of nomenclature to its logical conclusion and to have to change terms in the middle of a mouth.

Specimen numbers without prefixes belong to TMM; such numbers preceded by a hyphen are abbreviated, and include the five-digit locality number preceding, e.g., 40509-1, -2. All measurements are in millimeters. Interstitial wear is small and length measurements appear valid. Detailed descriptions of localities are on file at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, The University of Texas at Austin.

RELATIONSHIPS

Several types of upper molar teeth are found within the North American Uintan* artiodactyls (fig. 3). The upper molars are in the process of evolving toward selenodonty from an earlier condition of bunodonty. One of these types is illustrated by the protoreodontid molar tooth (fig. 3A). It was described by Gazin (1955) and further by Wilson (1971a). In this type of upper molar tooth during the Uintan there is a protoconule, strong para- and mesostyles, weak ribs, weak internal cingulum, and the postprotocrista meets the prehypocrista at right angles. With the loss of the protoconule and the development of a molariform P^4, this type of tooth evolves into that of *Agriochoerus.* This same type of tooth evolved into that found in the merycoidodonts by the loss of the protoconule and the development of enamel loops (fig. 3B) on the postero-external corner of the protoselene to form a selenodont molar.

A second type of artiodactyl upper molar tooth is also present during the late Bridgerian and Uintan and is best illustrated in *Leptotragulus* and *Leptoreodon* (fig. 3C). Their teeth have no protoconule, strong para- and mesostyles, strong ribs, well developed internal cingulum, and the postprotocrista is well developed, although it does not extend as far toward the ectoloph as does the prehypocrista. This is the most highly developed selenodont tooth of the Uintan.

A third type is found in *Oromeryx, Malaquiferus,* and *Eotylopus* (fig. 3D, E). These rather squat teeth have strong para- and mesostyles, very strong ribs, internal cingulum usually absent, and the protocone is bifurcate. There is no selene on the protocone.

The fourth type is exhibited by *Protylopus* in which there are strong para- and mesostyles, strong ribs, moderately strong internal cingulum, and the internal cones are either bifurcate or diagonal lophs that are directed in an anteroexternal to postero-internal direction.

A fifth type is represented by *Poebrodon* (fig. 3F) in which the para- and mesostyles are strong, the ribs strong, an internal cingulum weak, and the protoselene is as well developed as in *Leptoreodon.*

*I include Uinta A through Halfway (Wilson 1971a, fig. 6).

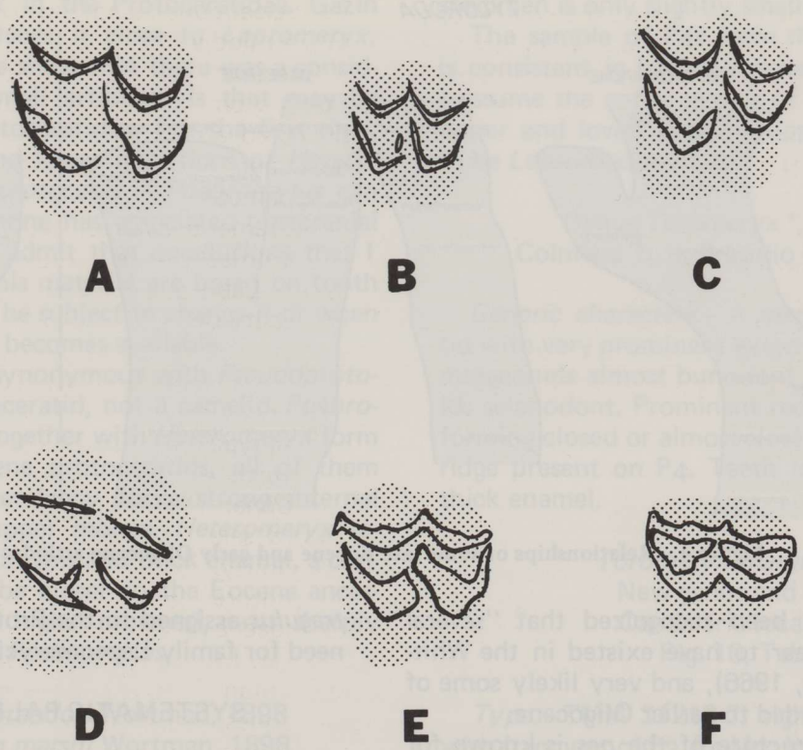


Figure 3.—Pattern on upper molar teeth showing degree of selenodonty in late Eocene and early Oligocene. *A. Protoreodon,* **late Eocene and early Oligocene, protoconule present, protoselene not developed.** *B. Bathygenys,* **early Oligocene, protoconule lost, loops developed for completion of protoselene.** *C. Leptoreodon,* **early late Eocene, protoselene well developed.** *D. Eotylopus,* **early Oligocene, T-shaped protoselene.** *E. Malaquiferus,* **late Eocene and early Oligocene, worn T-shaped protoselene.** *F. Poebrodon,* **late Eocene, well-developed selenodonty. Not to scale.**

The upper molars are narrower transversely than long. The latter character is unusual because the shape of the other types of molars are either square as *Malaquiferus* or wider transversely than long.

The upper teeth of a hypertragulid are not known in the late Uintan, so the roots of that family remain uncertain. In addition, no upper teeth of *Simimeryx* or *Hypertragulus* have yet been found in west Texas or Chihuahua, and, unfortunately, the upper teeth of *Hypisodus* from west Texas are badly worn. The upper teeth of some specimens, not all, from the Porvenir local fauna identified as *Leptomeryx* have non-bifurcate diagonal lophs that are directed in an anteroexternal to posterointernal direction across the protocone and hypocone. These lophs turn slightly posteroexternally to form incipient selenes (fig. 34). The pattern of the protocone is similar to that found in *Protoreodon.* In this character, a considerable proportion of the upper molars of *Leptomeryx* from the Porvenir local fauna are more primitive than those of *Leptoreodon* and *Leptotragulus* from the early Uintan.

I therefore disagree with Gazin (1955), as did Stirton (1967), that *Leptomeryx* is descended from either *Leptoreodon* or *Leptotragulus.* It seems much more logical to ally *Leptomeryx* with *Hypertragulus* and *Hypisodus.* As will be shown later, the west Texas specimens of *Leptomeryx* most closely resemble *Archaeomeryx,* and so I place *Leptomeryx* with the Hypertragulidae.

Either *Leptotragulus* or *Leptoreodon* in the Uintan could have been ancestral to *"Leptotragulus profectus"* and *Pseudoprotoceras longinares* (which will be shown to be a synonym of *Poabromylus kayi)* from the Chadronian. Such an affinity was mentioned by Gazin (1955), but he placed *Leptotragulus* and *Leptoreodon* in the Leptomerycidae as ancestors to *Leptomeryx.* For the reasons mentioned in the previous paragraph, I believe *Leptomeryx* cannot be a descendant of *Leptotragulus* or *Leptoreodon,* and for reasons pointed out later, I believe they are better allied with the Protoceratidae (fig. 4). Scott (1937) placed the sub-family Protoceratinae in the family Leptomerycidae, but the structure of the *pes* in protoceratids is not like that in hypertragulids. I see no need for a family Leptomerycidae.

It may disturb some that I have shown the Camelidae as having a polyphyletic origin. Perhaps when more has been published on the middle Tertiary camels, this will have to be modified. How-

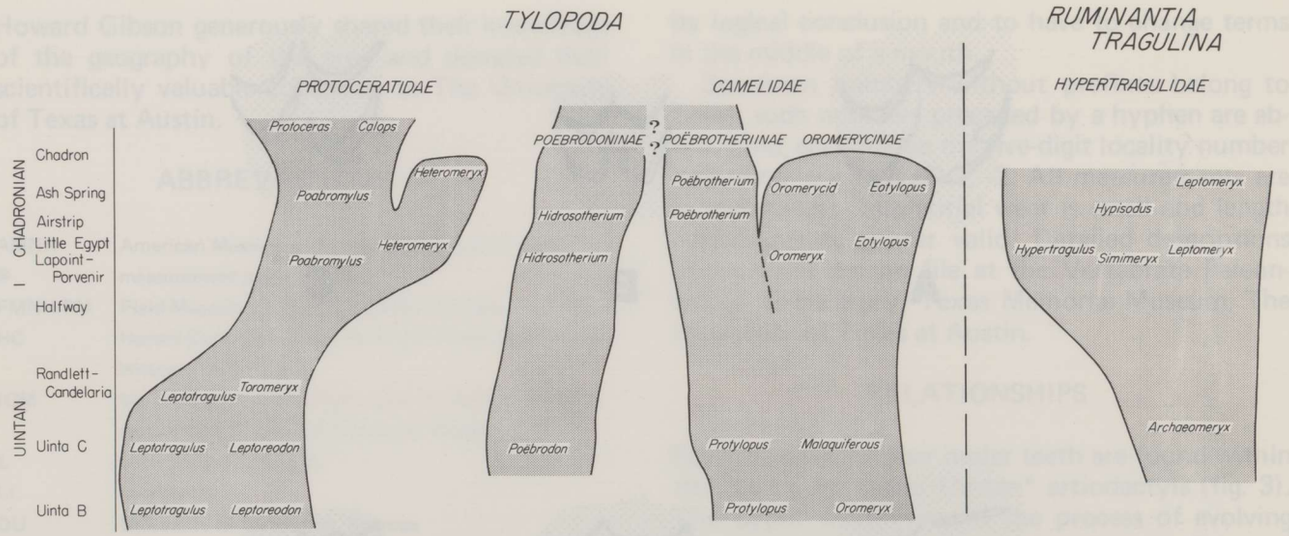


Figure 4.—Relationships of some late Eocene and early Oligocene artiodactyls

ever, it has long been recognized that "several camelid lines appear to have existed in the Whitneyan" (McKenna, 1966), and very likely some of these will be extended to earlier Oligocene.

The tylopod structure of the *pes* is known for *Protylopus* and *Leptoreodon* (Scott, 1899), *Eotylopus* (Matthew, 1910), and *Poebrotherium* (Scott, 1945), as well as for *Pseudoprotoceras* (Cook, 1934), *Protoceras* (Scott, 1940). I, therefore, follow Stirton (1967) and Patton and Taylor (1973) in placing the Protoceratidae in the Tylopoda. Colbert (1941) pointed out the traguloid condition of the fused cuboid-navicular in *Archaeomeryx* which adds further evidence for a relationship of *Leptomeryx* with the hypertragulids.

Individually, each of the types of upper molar teeth has long been recognized, but the lack of an adequate temporal succession of local faunas bridging the time span from Myton Uintan at approximately 45 million years to Orellan more than 10 million years later masked the time of first appearance and the method of development of each. The artiodactyl material from the Vieja Group has helped to bridge this gap in the record and permits a few observations about the classification of the major groups of North American artiodactyls.

In summary, unreduced dental arrangement of the merycoidodonts is so distinct and the dP4 so distinct from other major groups of artiodactyls that the rank of Suborder Oreodonta Osborn 1910 (Schultz and Falkenbach, 1968) is fully warranted. I follow Stirton (1967) and Patton and Taylor (1973) in placing the Protoceratidae in the Tylopoda because of the structure of the *pes.* Unlike Gazin (1955), I include *Leptoreodon* certainly and *Leptotragulus* not quite as certainly in an ancestral position in the Protoceratidae. I agree with Colbert (1941) that *Leptomeryx* is closely related to *Archaeomeryx* and is a hypertragulid. With the transfer of *Leptomeryx* and with *Leptoreodon* and *Leptotragulus* assigned to the Protoceratidae, there is no need for family Leptomerycidae.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla Owen, 1848
Suborder Tylopoda Illinger, 1811
Family Protoceratidae Marsh, 1891

Leptotragulus, Leptoreodon, Toromeryx (new genus), *Heteromeryx, Poabromylus, Calops, Protoceras, Syndyoceras, Prosynthetoceras, Synthetoceras, Paratoceras, Lambdoceras*

For reasons stated on page 5, I prefer to abandon the family Leptomerycidae and place *Leptomeryx* in the Hypertragulidae. Gazin (1955, pp. 81-82) describes the differences in the teeth of *Leptotragulus* and *Leptoreodon.* Such differences are primarily in the fourth lower premolar. It is impossible to distinguish the two genera on the basis of isolated upper or lower molars. For the Eocene material, I have depended on the presence of a prominent metaconid on P4 in order to identify *Leptoreodon.* Other characters such as the prominence of the paraconid, the closed or open talonid basin, the presence or absence of an entoconid, and the presence or absence of small accessory cuspules in the talonid are not reliable (fig. 5A-D).

Representatives of this family in the Oligocene are poorly known with the single exception of *Protoceras.* The genera *Pseudoprotoceras* and *Calops* have been referred to the family, but very little new has been written about them since their original description. *Heteromeryx* was described by Matthew (1905) and compared with hypertragulids. Simpson (1945) and Scott (1940) keep *Heteromeryx* in the Hypertragulidae and placed it close to *Leptomeryx,* as did Frick (1937). Romer (1966)

places *Heteromeryx* in the Protoceratidae. Gazin (1955, chart 1) places it close to *Leptomeryx.*

Several dentitions show that there was a considerable variety of small artiodactyls that may be referred to the Protoceratidae. For the first time, associated upper and lower dentitions of *Heteromeryx* and *Pseudoprotoceras = Poabromylus* can be identified, but none has associated postcranial elements. I readily admit that conclusions that I have drawn from this material are based on tooth characters and may be subject to change if or when postcranial material becomes available.

Poabromylus is synonymous with *Pseudoprotoceras* and is a protoceratid, not a camelid. *Poabromylus* and *Calops,* together with *Heteromeryx* form a group of Oligocene protoceratids, all of them with a persistent tendency for a strong internal cingulum on the upper molars. *Heteromeryx* retains low rounded crowns and thick enamel, a condition assumed to be closer to the Eocene ancestral forms than the higher crowned, more sharply selenodont cones of *Poabromylus.*

Genus *Leptoreodon* Wortman, 1898
Leptoreodon marshi Wortman, 1898
Whistler Squat and Candelaria local faunas
Figs. 5–9; Tables 1, 2

Synonyms.—Merycodesmus gracilis Scott, 1898; *Camelomeryx longiceps* Scott, 1898.

Type.—Skull and mandibles, AMNH 2064 from Uinta Fm., near White River, Uinta Basin, Utah.

Referred material.—TMM 40372-175, fragmentary palate with C-P^3, M^{1-3}, –10, P^3-M^1; –43, M^{2-3}; –44, P_2-M_3; –412, P_3-M_3; –417, alveoli for C and P_1, frag. P_2, P_3-M_3. Numerous isolated teeth and isolated postcranial material, all from the Whistler Squat l.f., are tentatively referred. TMM 40267-17, alveolus for P_1 and P_2-M_3; TMM 40689, frag. P^3, P^4, M^{2-3}, $\overline{C}$, P_{2-3}, from the Candelaria l.f.

Stratigraphic position.—Within the lower 50 feet of the Pruett Tuff, Buck Hill Group, Brewster County, Texas, Whistler Squat l.f. Within the lower 10 feet Colmena Tuff, Vieja Group, Presidio County, Texas, Candelaria l.f.

Age.—Early Uintan; Whistler Squat l.f. Uintan, Myton; Candelaria l.f.

Description.—Little can be added to the description given by Gazin (1955). A sample of six specimens of P_4, all from the same quarry, show the prominent metaconid. The selenes of the upper (fig. 6) and lower molars (fig. 7) are well developed. The internal cingula on the upper molars are prominent. Upper (fig. 8) and lower (fig. 9) deciduous dentitions are figured.

Relationships.—Leptoreodon (Hesperomeryx) edwardsi was described by Stock (1936). Table 2 shows measurements for *L. edwardsi* as compared with a small sample of *L. marshi.* The California specimen is only slightly smaller.

The sample of P_4s from the Whistler Squat l.f. is consistent in having a metaconid. On this basis, I assume the entire sample of isolated molars, both upper and lower and the upper dentition as well, to be *Leptoreodon marshi.*

Genus *Toromeryx*,* new genus
Colmena Tuff, Presidio County, Texas

Generic characters.—A medium-sized protoceratid with very prominent external cingula. Ento- and metaconids almost bunodont, proto- and hypoconids selenodont. Prominent recurved internal stylids forming closed or almost closed pockets. Metaconid ridge present on P_4. Teeth low and bulbous with thick enamel.

*Toromeryx marginensis***
New genus and species
Candelaria local fauna
Fig. 10, Table 3

Type.—TMM 31218-7, right mandible fragment with fragment of P_3. P_4-M_3; left mandible fragment with M_2-M_3 (fig. 8).

Stratigraphic position.—Three hundred feet below Buckshot Ignimbrite in Colmena Tuff.

Age.—Uintan, Myton, Late Eocene.

Diagnosis.—Same as for genus.

Description.—A medium-sized protoceratid with quite bunodont meta- and entoconids (fig. 10). The wear on these cusps occurs on the anterior surface first, leaving the posterior surface almost untouched as in *Pentacemylus.* External selenes well formed and separate through about half the tooth wear. External median pillars expanded into a triangle between the protoconid and hypoconid. External cingula prominent. Internal stylids prominent and recurved to form small cup-like depressions in the position of the para-, meta-, and entostylids. The recurved stylids give the meta- and entoconids a pinched look and exaggerate the rounded, bunodont pattern of those cusps. Similar cup-like stylids occur on the teeth of *Protoreodon petersoni* but its teeth are much more slender, higher crowned, and selenodont. The molar teeth of *Toromeryx* are brachydont, rather bulbous, and with thick enamel. The talonid is the only part of P_3 that is preserved. It shows a prominent external crest ending at the posteroexternal corner of the tooth. An internal crest originates from either a very broad protoconid or a metaconid ridge and the crest has a short externally directed bifurcation. The talonid is open posteriorly. P_4 does not have a prominent paraconid. There are well developed anteroexternal and anterointernal cingula. A metaconid crest leads in a posterointernal direction from the protoconid and

**Torus,* L. protuberance; *meryx,* G. ruminant
**From *marginatus,* L. border, in reference to the international border; *–ensis,* native to

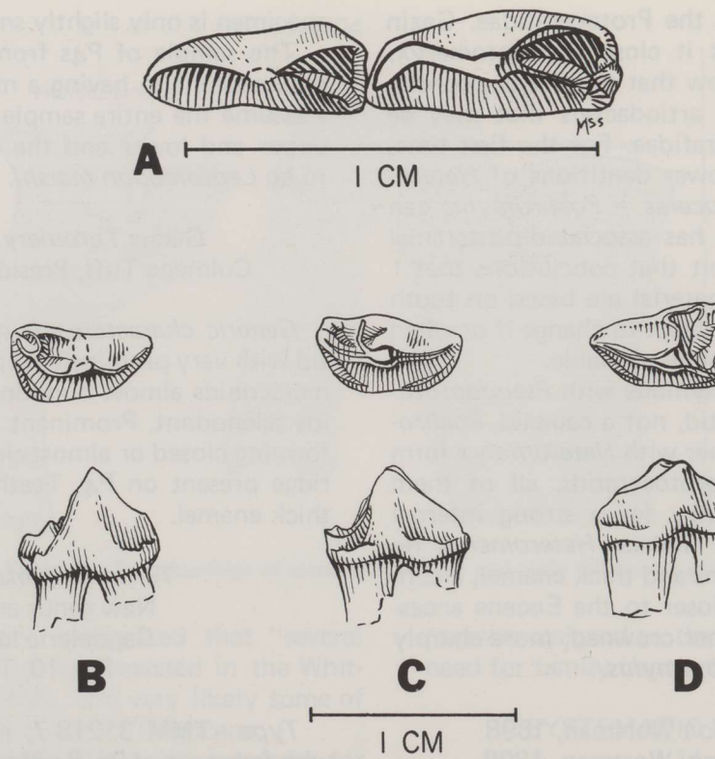


Figure 5.—Lower premolars, *Leptoreodon marshi*. *A*. TMM 40689, P_2, P_3. *B*. 41372-170, P_4 with posterointernal cusp and closed posterior basin. *C*. -220, P_4 without posterointernal cusp and open basin. *D*. -165, P_4 without posterointernal cusps. Whistler Squat l.f.

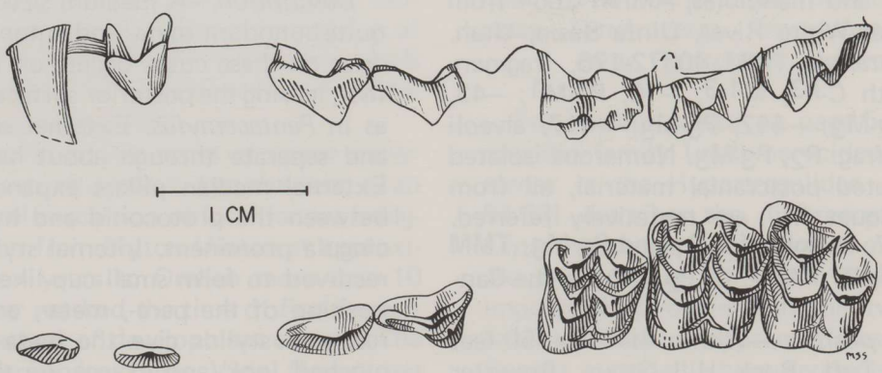


Figure 6.—*Leptoreodon marshi*, 41372-175. Skull fragment with C-P^3, M^{1-3}. External and occlusal views. Whistler Squat l.f.

then curves posteriorly to the posterointernal corner of the tooth. The main crest of the tooth passes posteriorly from the protoconid along the midline of the tooth then curves internally and almost closes the talonid basin. The talonid basin is found on the internal half of the tooth.

Questionable P^2 and P^3 are closely attached by matrix to the right mandible and it was impossible to prepare them free. Because it is uncertain that they belong with the same individual they are not included with the type.

Relationships.—Toromeryx seems to be an ancestor to *Heteromeryx*. The brachydont dentition with thick enamel is very distinctive. The rounded metaconid and entoconid bespeak its dicobunid ancestry and primitive condition. *Toromeryx* and *Heteromeryx* are the primitive members of the family Protoceratidae much as *Eotylopus* is a primitive member of the family Camelidae.

Genus *Heteromeryx* Matthew, 1905
Heteromeryx dispar Matthew, 1905
Porvenir local fauna
Figs. 11, 12; Tables 4, 5

Type.—AMNH 12326, skull with considerable part of the skeleton, most of the forefeet, and parts of the hind feet.

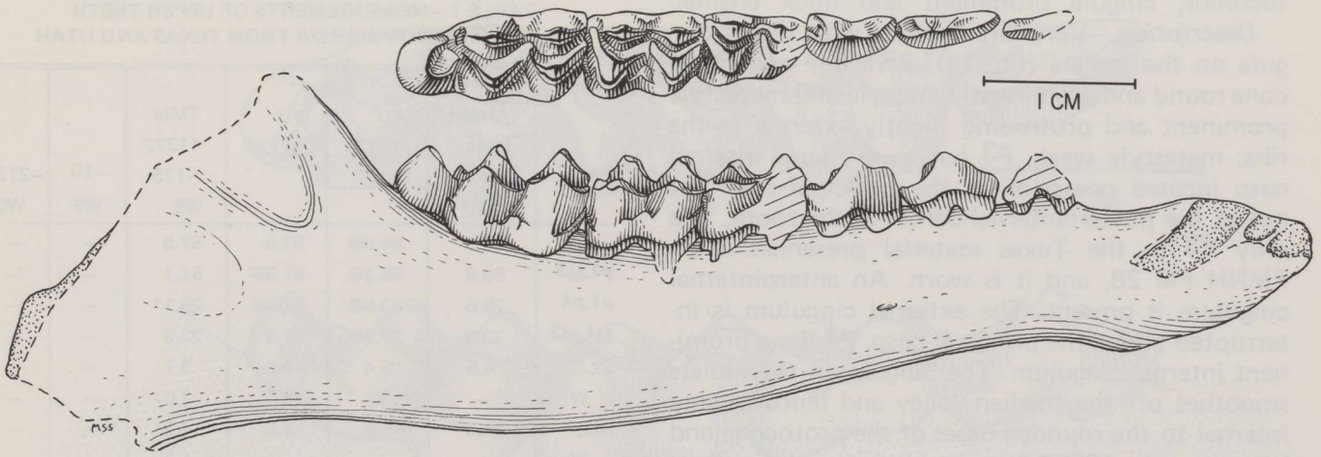


Figure 7.—*Leptoreodon marshi*, 41372-178. Lower jaw fragment with P_2-M_3. Occlusal and external views. Whistler Squat l.f.

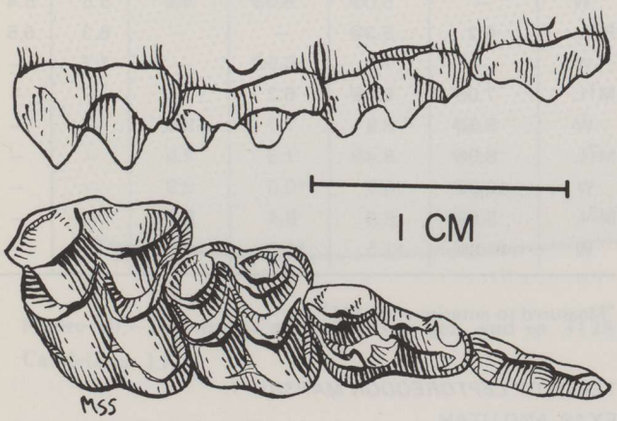


Figure 8.—*Leptoreodon marshi*, 41372-177. Skull fragment with dP^{2-4}, M^1. External and occlusal views. Whistler Squat l.f.

Referred material.—FMNH PM 28, right maxilla with half of P^2 and P^3-M^3; left maxilla with half of P^3, M^2-M^3; right mandible P_3-P_4 and half of M_1, half of M_2 and M_3; left mandible P_4 and broken M_1, apparently all from one individual; FMNH PM 40, left mandibular ramus with M_2 and broken M_3 and right mandibular ramus with posterior half of P_3 and anterior half of P_4 and heel of M_3. TMM 40203-7, right maxilla with P^4 and internal halves of M^1 and M^2; 40203-24, right M^3 and posterior half of M^2. 40203-14, left M^3. 40203-43, right M_1. 40203-10, posterior half of right M_3.

Stratigraphic position.—Within the lower 25 feet of Chambers Tuff Formation, Vieja Group; Porvenir l.f.

Age.—Early Chadronian.

Diagnosis.—Small, very brachydont, broad cingula on upper molars, thick enamel. Lower molars with low, narrow, oval-shaped metaconids and en-

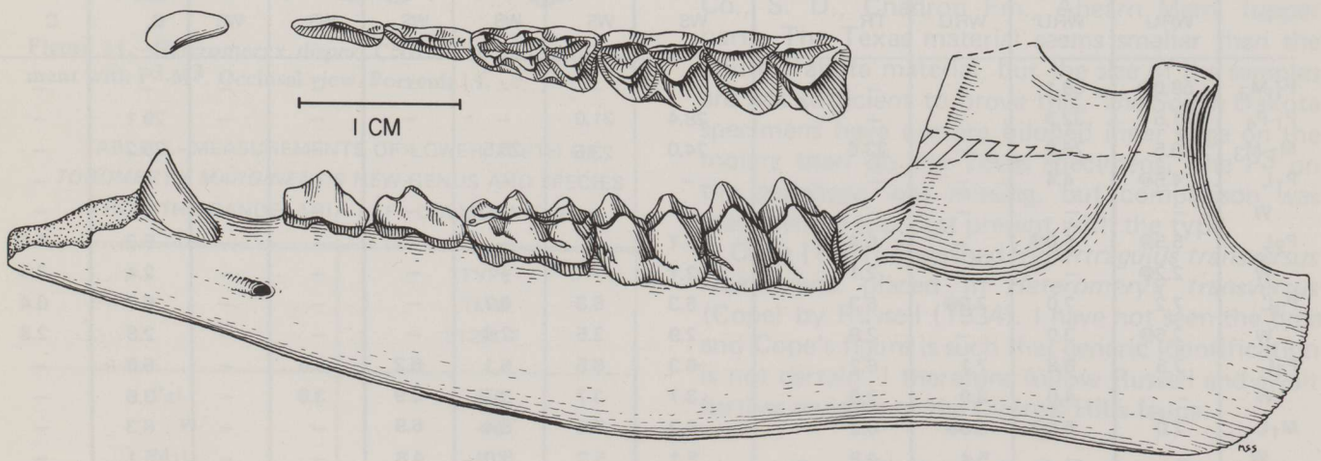


Figure 9.—*Leptoreodon marshi*, 41372-176. Lower jaw fragment with dP^{1-4}, M^{1-2}. Occlusal and external views. Whistler Squat l.f.

toconids, cingula prominent and thick enamel.

Description.—Very brachydont with broad cingula on the molars (fig. 11). Paracone and metacone round and prominent. Parastyle and mesostyle prominent and protruding slightly external to the ribs; metastyle weak. P^3 has a very large internal cusp located posterior to the principal cusp but not at the posterointernal corner of the tooth. The only P^3 in the Texas material preserved is on FMNH PM 28, and it is worn. An anterointernal cingulum is present. The external cingulum is interrupted above the principal cusp. P^4 has a prominent internal cingulum. The cingula on the molars smoothes off the median valley and tends to stay internal to the rounded bases of the protocone and hypocone. In 40203-7, a double internal cingulum is present on the anterior and medial edges of all three upper molars, a condition that is prominent in *Poabromylus.*

In the lower teeth, P_3 and P_4 in FMNH PM 28 (fig. 12) are worn. However, P_3 does not appear to have had a paraconid. There is no entoconid on P_3 or P_4. Both teeth are broad. The molars have low, narrow, oval-shaped metaconids and entoconids. The cingula are prominent and may or may not be continuous around the protoconid and hypoconid. In 40203-43, an M_1, the cingulum is double. Between the protoconid and hypoconid there is a triangular expansion of the cingulum separated from the bases of the protoconid and hypoconid.

TABLE 1.—MEASUREMENTS OF UPPER TEETH OF *LEPTOREODON MARSHI* FROM TEXAS AND UTAH

	TYPE AMNH 2064 WRU	PU 11225	PU 11226	TMM 41372 –175 WS	–10 WS	–212 WS
C-M^2	58.0	64.0@	57.5	57.5	–	–
P^1-M^3	50.8	55.2@	51.5@	51.1	–	–
P^1-P^4	29.5	33.5@	31.0@	29.1*	–	–
M^1-M^3	23.0	22.5@	21.9	22.3	–	–
CL	4.5	5.4	4.5	3.7	–	–
W	–	3.2	3.0	2.0	–	–
P^1L	4.5	5.0	3.5	4.2	–	–
W	–	–	–	1.7	–	–
P^2L	6.5	7.0@	6.9	7.2	–	–
W	–	–	2.5	3.7	–	–
P^3L	7.3@	7.0@	7.0	6.5	6.9	–
W	–	5.0@	6.0@	4.6	5.5	5.4
P^4L	6.2	5.3@	–	–	6.3	6.5
W	–	7.0	6.5@	–	7.2	–
M^1L	7.0@	6.6@	6.2	7.1	–	–
W	8.5@	8.9	7.7	8.0	–	–
M^2L	8.0@	8.4@	7.3	7.5	–	–
W	10.0@	10.5	10.3	8.9	–	–
M^3L	8.6@	8.9	8.4	8.8	–	–
W	11.0@	11.5	11.6	10.2	–	–

*Measured to anterior end of M^1

TABLE 2.—MEASUREMENTS OF LOWER TEETH OF *LEPTOREODON MARSHI* FROM CALIFORNIA, TEXAS, AND UTAH

	TYPE AMNH 2064 WRU	PU 11225 WRU	USNM 20397 WRU	*L. EDWARDSI* CIT 1840 TR	TMM 41372 –44 WS	–417 WS	–412 WS	–419 WS	–391 WS	–395 WS	40276 –17 C	40689 C
P_1-M_3	58.0@	58.1	–	–	–	–	–	–	–	–	–	–
P_1-P_4	31.5	32.3	–	–	28.4	31.0	–	–	–	–	29.1	–
M_1-M_3	26.5	26.0	–	23.6	24.0	23.5	25.5	–	–	–	25.2	–
P_1L	4.5@	4.4	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–	–	–
P_2L	5.5@	5.0@	–	5.4	5.1	–	–	–	–	–	5.3	5.5
W	2.2@	–	–	2.1	2.1	–	–	–	–	–	2.4	2.4
P_3L	7.2	7.0	7.0@	6.3	6.3	6.8	6.7	–	–	–	6.7	6.4
W	2.5@	3.0	–	2.9	2.9	2.5	2.6	–	–	–	2.8	2.8
P_4L	7.5	6.8	7.1	6.2	6.3	6.5	6.1	6.2	6.5	–	6.8	–
W	–	4.0	3.9	3.6	3.7	3.7	3.7	3.9	3.8	–	3.6	–
M_1L	7.0	6.6@	6.8@	6.2	6.3	5.8	6.4	6.9	–	–	6.3	–
W	–	–	5.4	4.8	5.1	5.2	5.0	4.8	–	–	5.1	–
M_2L	8.0	7.8	8.2	7.6	7.4	7.0	7.6	–	–	7.4	7.1	–
W	–	6.0	6.4	5.9	5.7	6.0	5.1	–	–	6.7	6.0	–
M_3L	11.6	12.0@	–	10.3	11.1	10.9	11.6	–	–	11.2	11.7	–
W	–	6.3	6.8	5.7	6.4	6.3	6.0	–	–	6.2	6.3	–

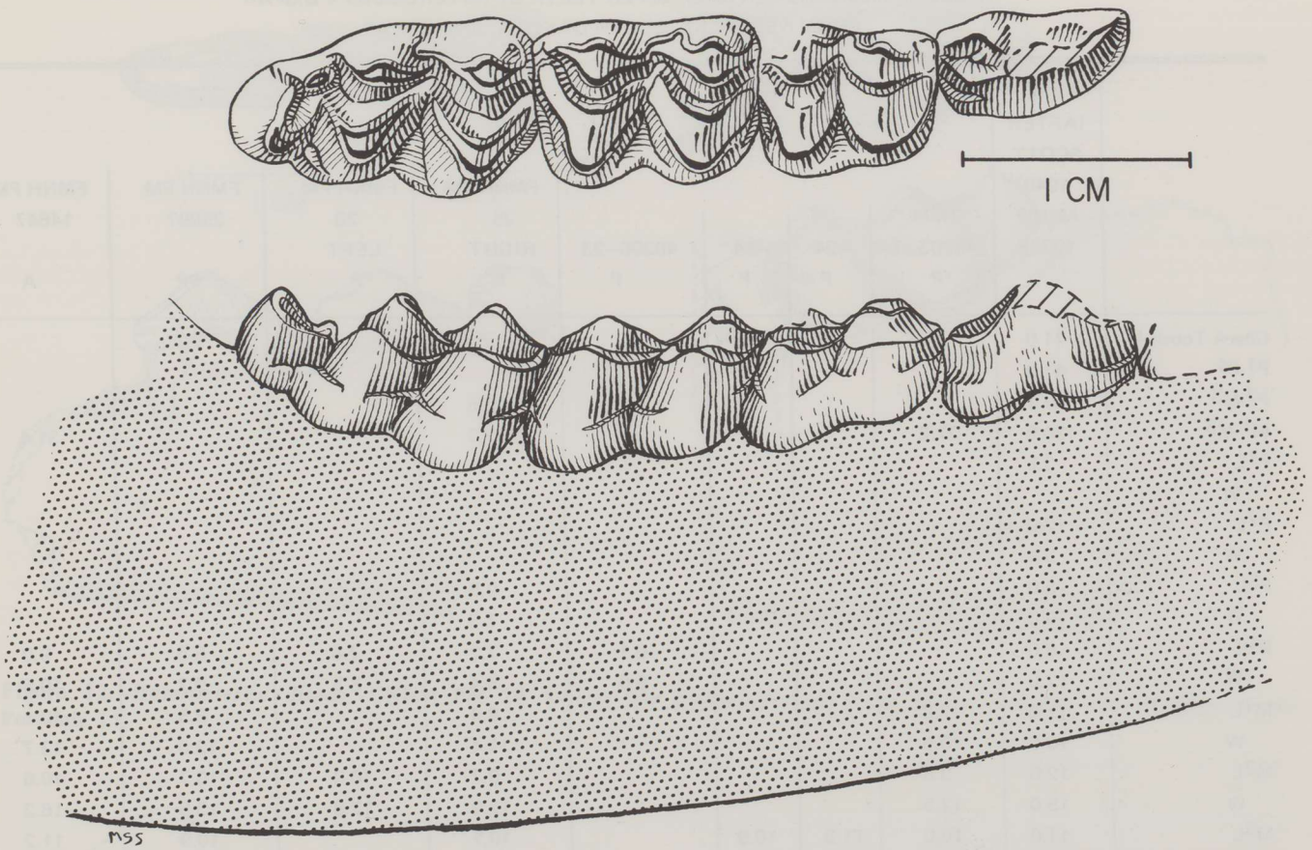


Figure 10.—*Toromeryx marginensis* **n. gen. and sp. 31281-7. Lower jaw fragment with P_4-M_3. Occlusal and external views. Candelaria l.f.**

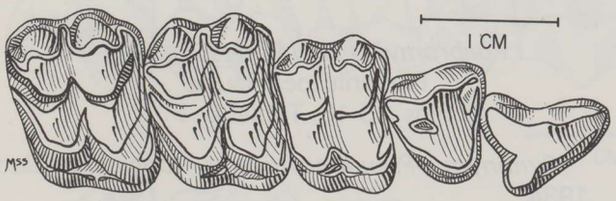


Figure 11.—*Heteromeryx dispar*, **CNHM PM 28. Skull fragment with P^3-M^3. Occlusal view. Porvenir l.f.**

TABLE 3.—MEASUREMENTS OF LOWER TEETH OF *TOROMERYX MARGINENSIS* NEW GENUS AND SPECIES FROM THE CANDELARIA L. F., COLMENA TUFF

	TYPE TMM 31281-7
P_4L	8.6
W	4.8
M_1L	8.0
W	6.2@
M_2L	9.0
W	7.0
M_3L	14.1
W	7.1

Relationships.—Two additional specimens of *Heteromeryx dispar* are included here for the record: FMNH PM 25897 from the Henry Morgan Quarry, NE ¼, Sec. 23, T33N, R53W, Sioux Co., Nebraska, Chadron Fm. (probably Peanut Peak Mem.), 60 feet below capping sandstone; and FMNH PM 14647, Collection 33, Battle Creek Breaks, Custer Co., S. D., Chadron Fm., Ahearn Mem. (upper part). The Texas material seems smaller than the South Dakota material, but the size of the samples are not sufficient to prove this. The South Dakota specimens have a more bilobed inner edge on the molars than do the Texas specimens. The P^3 on the genotype was missing, but comparison was made with a wax cast present with the type.

Cope (1891) described *Hypertragulus transversus* which was placed in *Heteromeryx transversus* (Cope) by Russell (1934). I have not seen the type and Cope's figure is such that generic identification is not certain. I therefore follow Russell and await further revision of the Cypress Hills fauna.

Genus *Poabromylus* Peterson, 1931

Synonym.—Pseudoprotoceras Cook, 1934.

Type.—Poabromylus kayi Peterson, 1931

Generic characters.—P_4 with strong metaconid either separate or connected by a posterointernally

TABLE 4.—MEASUREMENTS OF UPPER TEETH OF *HETEROMERYX DISPAR* FROM NEBRASKA, SOUTH DAKOTA, AND TEXAS

	TYPE (AFTER SCOTT 1940) AMNH 12326	TMM 40203–7 P	–24 P	–14 P	40206–23 P	FMNH PM 28 RIGHT P	FMNH PM 28 LEFT P	FMNH PM 25897 PP	FMNH PM 14647 A
Cheek Tooth L	71.0								
P^1-P^4	41.0								
P^2-M^3	49.1					43.6			
M^1-M^3	30.0	27.2				27.3			31.4
P^1 L	3.5								
W									
P^2 L	12.0								
W	5.5								
P^3 L	9.0					9.5			
W	10.0					7.3			
P^4 L	8.0				6,1	7.2	7.8	8.5	9.0
W	12.0				8.0	8.4	8.5	9.7	10.5
M^1 L	11.0	7.8				8.4		8.5	10.1
W	13.0	10.6				11.4		12.0	13.7
M^2 L	12.0	9.5				9.7	10.0	10.7	10.6
W	15.0	12.5				12.9	12.8	13.8	16.2
M^3 L	11.0	10.0	11.3	10.9		10.7		10.9	11.2
W	14.5	12.8	14.7	13.4		13.4	13.5	13.4	14.5

directed ridge to the protoconid. Posterior crests from protoconid widely open posteriorly on P_4 but narrow on P_3. Talonid of P_4 open or closed, closed in type. Paraconid as a crest not a prominent cusp. P_4 short and broad. Lower molars selenodont, usually with median pillars. Upper molars with strong internal cingula; selenodont, valleys deeper, enamel thinner than in *Heteromeryx.*

TABLE 5.—MEASUREMENTS OF LOWER TEETH OF *HETEROMERYX DISPAR* FROM PORVENIR LOCAL FAUNA, CHAMBERS TUFF

	FMNH PM 40	FMNH PM 28	FMNH PM 28	TMM 40203–7
P_1 L				
W				
P_2 L				
W				
P_3 L			9.8	
W			4.2	
P_4 L		9.4	8.7	
W		5.4	5.2	
M_1 L				10.3
W				7.8
M_2 L	10.5			
W	9.2			
M_3 L			15.8	15.0
W			9.3	7.9

Poabromylus kayi Peterson, 1931
Porvenir local fauna
Figs. 13-16; Tables 6, 7

Synonym.—Pseudoprotoceras longinaris Cook, 1934.

Type.—CM 11753, left ramus of lower jaw with alveoli for P_2, P_3-M_3, from Lapoint Member, Duchesne River Formation, 11 miles west of Vernal, Uinta County, Utah.

Referred material.—AMNH 81000 (HC 507), type of *Pseudoprotoceras longinaris;* FMNH PM 26257, R P^2-M^3, fragmentary R P_3 and P_4, M_{1-3}; FMNH PM 25896, R P_3-M_3, FMNH PM 26258, R P^3-M^3, M_1-M_3 fragment; FMNH PM 20736, L P_4-M_3 fragment; FMNH PM 25893, L P_4-M_3; FMNH PM 25891, R P_3-M_2; FMNH PM 20729, L P^3-M^3; FMNH PM 20727, R dP^3, dP^4-M^2; FMNH PM 14649, R dP_2 fragment, dP_3, dP_4, M_1, M_2 fragment, M_3; FMNH PM 20735, R dP_4, M_1-M_3; and numerous isolated teeth from localities in the Chadron Fm. of South Dakota; SDSM 5349, R P^2-M^3; SDSM 5342, L P_3-M_3; L dP_2. dP_3, dP_4, M_1; SDSM 5340, L P_1-P_4; all SDSM specimens from the Yoder Fm., Goshen Co., Wyo.; TMM 40206-38, fragmentary L M^1, M^2-M^3; TMM 40206-39, frag-

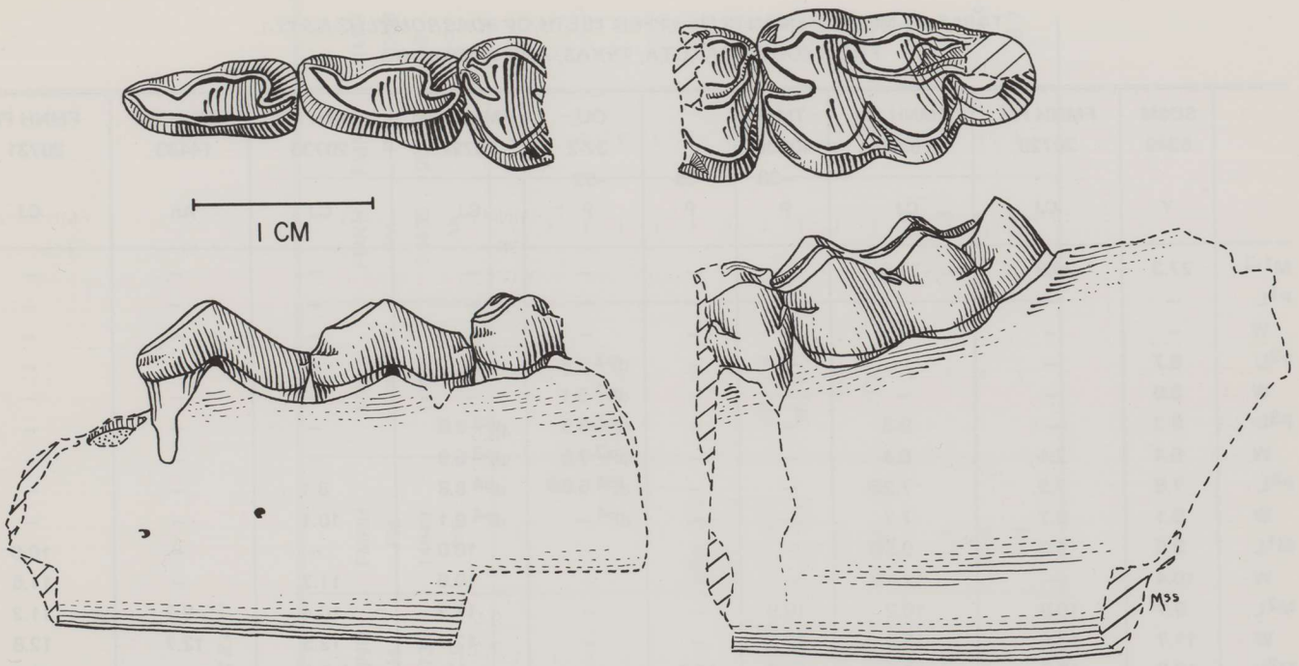


Figure 12.—*Heteromeryx dispar*, **CNHM PM 28. Lower jaw fragments with P_{3-4}, M_{1-3}. External and occlusal views. Porvenir l.f.**

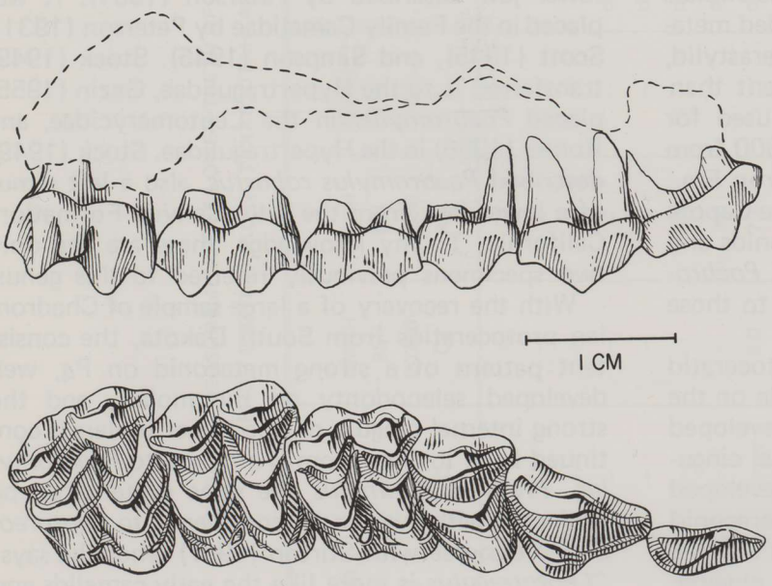


Figure 13.—*Poabromylus kayi*, **FMNH PM 26257. Skull fragment with RP^{2-4}, M^{1-3}. External and occlusal views. Chadron Fm., top Crazy Johnson Mem., Pennington Co., S. D.**

mentary R M^{2}-M^{3}, TMM 40206-9, R and L M_3; OU 22-2-52, L dP^2, dP^3, dP^4, M^1 and fragment M^2; FMNH PM 455, fragmentary L P_4, M_1-M_3, all from Porvenir l.f., Chambers Tuff, Presidio Co., Tex.

Stratigraphic distribution.—The type is from the Lapoint Member of the Duchesne River Fm., Uinta Co., Utah (Peterson, 1931). The type of *Pseudoprotoceras longinaris* is from the Lower Chadron Formation near Crawford, Nebraska (Cook, 1934).

Age.—The referred material from Wyoming, South Dakota, and Texas is all early Chadronian.

Diagnosis.—Very prominent metaconid on P_4 as in *Leptoreodon.* The metaconid may be separate from the protoconid or connected by a prominent posterointernally directed ridge. The direction of the aforementioned ridge from the protoconid to the metaconid and the direction of the ridge from the protoconid to the hypoconid are such that there is a broad open groove between them. A groove in the same position on the P_4 of *Poebrotherium* is narrow because there is no metaconid in *Poebrotherium.* The P_3 of *Poabromylus* lacks the metaconid and hence is more like the P_4 of *Poebrotherium.* P_2 does not have as well developed

TABLE 6.—MEASUREMENTS OF UPPER TEETH OF *POABROMYLUS KAYI* FROM SOUTH DAKOTA, TEXAS, AND WYOMING

	SDSM 5349	FMNH PM 20729	FMNH PM 26285	TMM 40206 –38	–39	OU 27-2 –52	FMNH PM 20727	FMNH PM 20730	FMNH PM 14433	FMNH PM 20731
	Y	CJ	CJ	P	P	P	CJ	CJ	Ah	CJ
M^{1-3}	27.3	29.9	27.8	–	–	–	–	–	–	–
P^1L	–	–	–	–	–	–	–	–	–	–
W	–	–	–	–	–	–	–	–	–	–
P^2L	8.7	–	–	–	–	dP^2 7.8	–	–	–	–
W	3.9	–	–	–	–	dP^2 3.1	–	–	–	–
P^3L	9.3	–	9.3	–	–	dP^3 8.5	dP^3 9.8	–	–	–
W	6.4	7.1	6.4	–	–	dP^3 7.0	dP^3 6.9	–	–	–
P^4L	7.8	7.2	7.2@	–	–	dP^4 6.8@	dP^4 8.8	8.1	–	–
W	9.1	8.7	7.7	–	–	dP^4 –	dP^4 9.1	10.1	–	–
M^1L	8.5	9.6	9.5@	–	–	–	10.0	–	–	10.6
W	10.4	–	11.1@	–	–	–	10.6	11.7	–	11.5
M^2L	9.7	10.8	10.2	10.9	–	–	11.2	10.4	9.7	11.2
W	11.7	13.6	13.0	12.3	–	–	12.7	12.5	12.7	12.8
M^3L	10.2	10.5	10.3	10.5	10.5	–	–	10.8	–	11.3
W	12.1	12.6	–	11.9	11.8	–	–	12.2	–	13.0

posterointernal crest as P_3. There is a diastema between P_1 and P_2. P_1 is caniniform. The molars fully selenodont (fig. 14) with more rounded meta- and entoconids than in *Poebrotherium.* Parastylid, metastylid, and entostylid more prominent than on *Poebrotherium.* The *Poebrotherium* used for comparison are specimens FMNH PM 25800 from probable Peanut Peak Mem. of the Chadron Fm., and TMM 40504-149 (figs. 25, 26) from the Capote Mountain Tuff, Vieja Group. The metaconids and entoconids of contemporary, Chadronian, *Poebrotherium* are already blade-like in contrast to those of *Poabromylus.*

The upper teeth (figs. 13, 16) are protoceratid with very highly developed internal cingula on the molars. P^2 is long and narrow with a well developed or poorly developed paraconid and internal cingulum. P^3 has a prominent internal cusp developed on a prominent internal cingulum. The paraconid on P^3 is well or poorly developed. P^4 has a single external cusp and anterior and posterior cingula. The molars are fully selenodont but not high-crowned. Internal cingula and median pillars very strong. Prominent ribs and para-, meso-, and metastyles. Skull as described in Cook (1934) and tarsal elements not fused (Cook, 1934).

The discovery of associated upper and lower dentitions (figs. 13, 14) by Clark in the Chadron Formation of South Dakota permits me to synonymize *Poabromylus* and *Pseudoprotoceras* with relative certainty. Little more can be added to the descriptions of Gazin (1955), Peterson (1931), and Cook (1934) other than to emphasize those characters that are useful for distinguishing *Poabromylus* from *Poebrotherium* as I have tried to do above.

Relationships.—The type is a left ramus of the lower jaw described by Peterson (1931). It was placed in the Family Camelidae by Peterson (1931), Scott (1945), and Simpson (1945). Stock (1949) transferred it to the Hypertragulidae, Gazin (1955) placed *Poabromylus* in the Leptomerycidae, and Romer (1966) in the Hypertragulidae. Stock (1949) described *Poabromylus robustus,* also a left ramus of a lower jaw, from the Titus Canyon Formation, California. To my knowledge, these are the only two specimens previously referred to this genus.

With the recovery of a large sample of Chadronian protoceratids from South Dakota, the consistent pattern of a strong metaconid on P_4, well developed selenodonty on the molars, and the strong internal cingula on the upper molars is continued back in time from *Protoceras* to *Poabromylus.* From *Poabromylus* the same pattern can be projected with even more confidence to *Leptoreodon.* I disagree with Stirton (1967) where he says: "*Leptotragulus* is more like the early camelids and protoceratids than *Leptoreodon* (and in part *Poabromylus)* . . . ." I believe that *Leptoreodon* is definitely a small protoceratid and further that neither *Leptotragulus* nor *Leptoreodon* has anything to do with the early camels. The presence of a metaconid on P_4 of *Protylopus* and *Eotylopus* is offset by differences in the degree of selenodonty of the upper molars of *Protylopus, Eotylopus,* and as will be pointed out (p. 22), the primitive stage of selenodonty in the early Chadronian *Poebrotherium. Leptoreodon* and *Leptotragulus* had well developed selenodont molars by the early Uintan, if not earlier, whereas this character is not achieved in *Poebrotherium* until the early Chadronian.

TABLE 7.–MEASUREMENTS OF LOWER TEETH OF *POABROMYLUS KAYI* FROM SOUTH DAKOTA, TEXAS, UTAH, AND WYOMING

	TYPE *P. kayi* CM11753 L	TITUS C. TYPE *P. robustus* C348	SDSM 5342 Y	FMNH PM 26257 CJ	FMNH PM 20736 CJ	FMNH PM 25896 Ah	FMNH PM 455 P	SDSM 5347 Y	FMNH PM 20735 CJ	FMNH PM 14649 Ah	FMNH PM 14434 Ah	FMNH PM 14435 Ah	FMNH PM 20801 CJ	TMM 40206 –9 P
P_2-P_4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M_1-M_3	35.5	–	32.1	31.9	–	–	–	–	–	–	–	–	–	–
P_2-M_3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P_2L	–	–	–	–	–	–	–	dP^2 6.9	–	–	–	–	–	–
W	–	–	–	–	–	–	–	dP^2 2.3	–	–	–	–	–	–
P_3L	8.7	8.5@	9.3	–	–	8.4	–	dP^3 7.6	–	dP_3 8.5	–	–	–	–
W	3.3	3.6	4.0	–	–	3.0	–	dP^3 3.0	–	dP_3 3.2	–	–	–	–
P_4L	8.6	–	8.1	–	9.0	7.4	–	dP^4 10.0	dP_4 11.2	dP^3 10.0	dP_4 9.8	–	–	–
W	5.1	–	5.2	4.8	5.3	4.8	–	dP^4 5.0	dP_4 –	dP^4_4 5.5	dP_4 6.0	–	–	–
M_1L	8.8	–	8.5	8.6	10.1	8.5	–	8.4	9.1	8.0	7.3	–	9.0	–
W	6.2@	–	7.7	7.1	8.0	–	–	6.8	7.2	6.8	7.2	–	7.4	–
M_2L	10.5@	11.5	9.2	9.6	10.2	9.8	8.5	–	12.0	–	–	9.5	–	–
W	–	9.9	8.3	7.5	9.2	7.7	6.8	–	8.3	7.3	–	7.3	–	–
M_3L	16.7	17.3	14.4	13.8	–	14.3	13.1	–	–	13.4	–	13.4	–	15.4
W	8.5	10.5	7.6	7.5	–	8.1	6.8	–	–	7.4	–	7.5	–	8.7

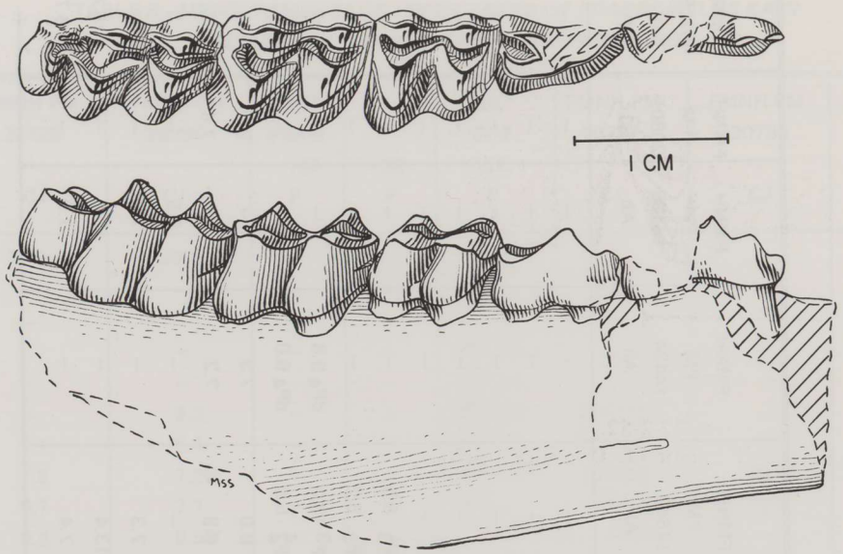


Figure 14.—*Poabromylus kayi,* **FMNH PM 26257. Lower jaw fragment with fragmentary RP_3, P_4, M_{1-3}. Occlusal and external views. Chadron Fm., top Crazy Johnson mem., Pennington Co., S. D.**

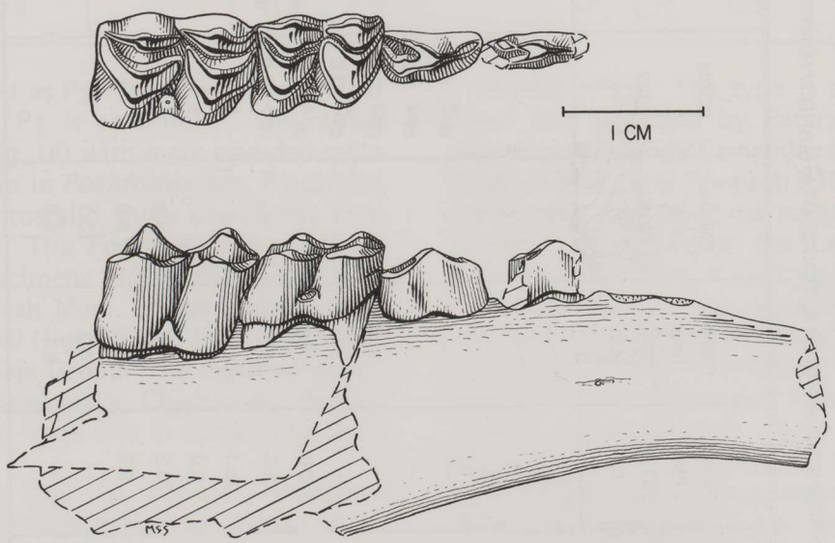


Figure 15.—*Poabromylus kayi,* **FMNH PM 25891. Lower jaw fragment with fragmentary RP_3, P_4, M_{1-2}. Occlusal and external views. Chadron Fm., ?Peanut Peak Mem., Henry Morgan Quarry, Sioux Co., Nebr.**

The large sample of *Leptoreodon* from the Whistler Squat l.f. demonstrates that the size increases from *Leptoreodon* of the Uintan to *Poabromylus* of the Chadronian are not as great as from *Poabromylus* of the Chadronian to *Protoceras* of the Orellan.

Poabromylus minor new species
Porvenir local fauna
Fig. 17; Tables 8, 9

Type.—SDSM 5341, left maxillary fragment with P^3-M^3 from Yoder Fm., Goshen Co., Wyoming (fig. 17).

Material.—TMM 40506-23, right maxillary fragment with P^4 and fragmentary M^{1-2}, OU 22-2-52, left maxillary fragment with fragmentary M^1 and M^{2-3}; FMNH PM 20069, left P^{3-4}; FMNH PM 101 M_3; TMM 40203-15, fragmentary M_2 and M_3; —27, fragmentary dP_4, M_{1-2}.

Stratigraphic position.—From 5—50 feet above Buckshot Ignimbrite in lower part of Chambers Tuff; Porvenir l.f., Presidio Co., Texas; Quarry 1 of South Dakota School of Mines and Technology, Yoder Fm.; and Granath Quarry, Collection 30, Peanut Peak Mem., Chadron Fm., Shannon Co., South Dakota.

Age.—Early Chadronian.

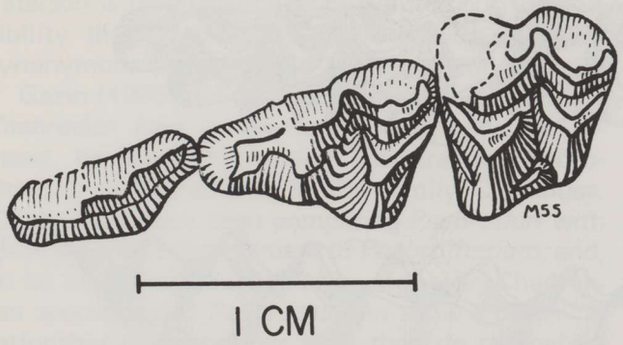


Figure 16.—*Poabromylus kayi*, **OU 22-2-52. Skull fragment with LdP$^{2-4}$. Occlusal view. Porvenir l.f. Chambers Tuff.**

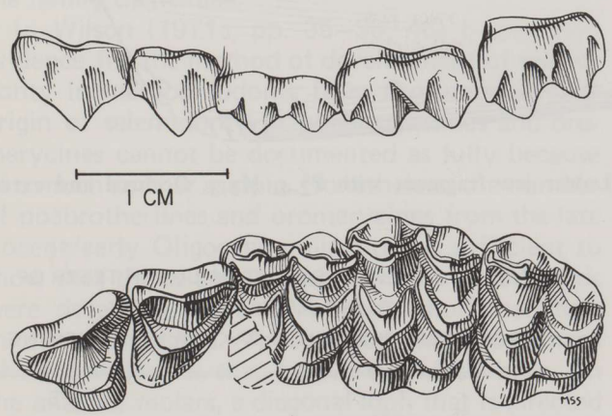


Figure 17.—*Poabromylus minor* **n. sp., type, SDSM 5341. Skull fragment with LP$^{3-4}$, M$^{1-3}$. External and occlusal views. Yoder Fm., Goshen Co., Wyo.**

TABLE 8.—MEASUREMENTS OF UPPER TEETH OF *POABROMYLUS MINOR* NEW SPECIES, FROM SOUTH DAKOTA AND TEXAS

	TYPE SDSM 5341 Y	OU 22-2-52 P	TMM 40206-23 P	SDSM 53296 Y	FMNH 20069 PP
M^{1}-M^{3}	25.5	–	–	–	7.1
P^{3}L	8.3	–	–	dP^{3} 10.2	6.0
W	6.6	–	–	dP^{3} 6.6	5.8
P^{4}L	6.7	–	5.6	dP^{4} 8.1	7.1
W	8.0	–	8.0	dP^{4} 8.6	–
M^{1}L	8.7	–	–	8.3	–
W	–	–	–	10.3	–
M^{2}L	9.2	7.7	–	–	–
W	12.1	9.8	–	–	–
M^{3}L	8.7	7.5	–	–	–
W	11.8	9.6		–	–

TABLE 9.—MEASUREMENTS OF LOWER TEETH OF *POABROMYLUS MINOR* NEW SPECIES FROM SOUTH DAKOTA AND TEXAS

	TMM 40203-27	TMM 40203-15	FMNH PM 101
P$_{2}$-M$_{3}$	–	–	–
P$_{2}$-P$_{4}$	–	–	–
M$_{1}$-M$_{3}$	–	–	–
P$_{2}$L	–	–	–
W	–	–	–
P$_{3}$L	–	–	–
W	–	–	–
P$_{4}$L	–	–	–
W	–	–	–
M$_{1}$L	6.9	–	–
W	6.1	–	–
M$_{2}$L	8.2	–	–
W	6.7	–	–
M$_{3}$L	–	12.1	13.2
W	–	7.4	7.5

Diagnosis.—Smaller than *Poabromylus kayi.* Strong internal cingula on upper molars. P^{3} short and broad without separate paracone. Lower premolars unknown.

Description.—A small species of *Poabromylus.* The third upper premolar is very distinctive in that it is shorter and wider than that of *P. kayi.* The internal cingulum is prominent and forms a larger internal cusp than that found in *P. kayi.* The P^{3} of *P. kayi* is long and narrow as compared to the same tooth in *P. minor.* This and the smaller size would probably make for a shorter muzzle. The other teeth show no differences with *P. longinaris.*

Relationship.—It is disconcerting to find two very similar sets of P^{4}-M^{3} preceded by such very different P^{3}s. The upper premolars of *P. kayi* are smaller but structurally like those of *Protoceras* and *Leptoreodon* but the P^{3} of *P. minor* is unlike that of either. The upper third premolar is more like that one would expect as ancestral to *Prosynthetoceras* of the Miocene. Unfortunately, the upper dentition of the intermediate *Syndyoceras* has not been figured, so that its relationships could not be determined. Hopefully, when the lower premolars of this species are found, they will bear out my reference to *Poabromylus.* The size difference and the very different P^{3} are felt to warrant a new species.

"Leptotragulus profectus"
Fig. 18; Table 10

In 1903 Matthew described *"Leptotragulus profectus"* from the Pipestone Springs locality of Montana. The type consists of P$_{2-4}$ and broken M$_{1}$. Associated with the type were fragments of other

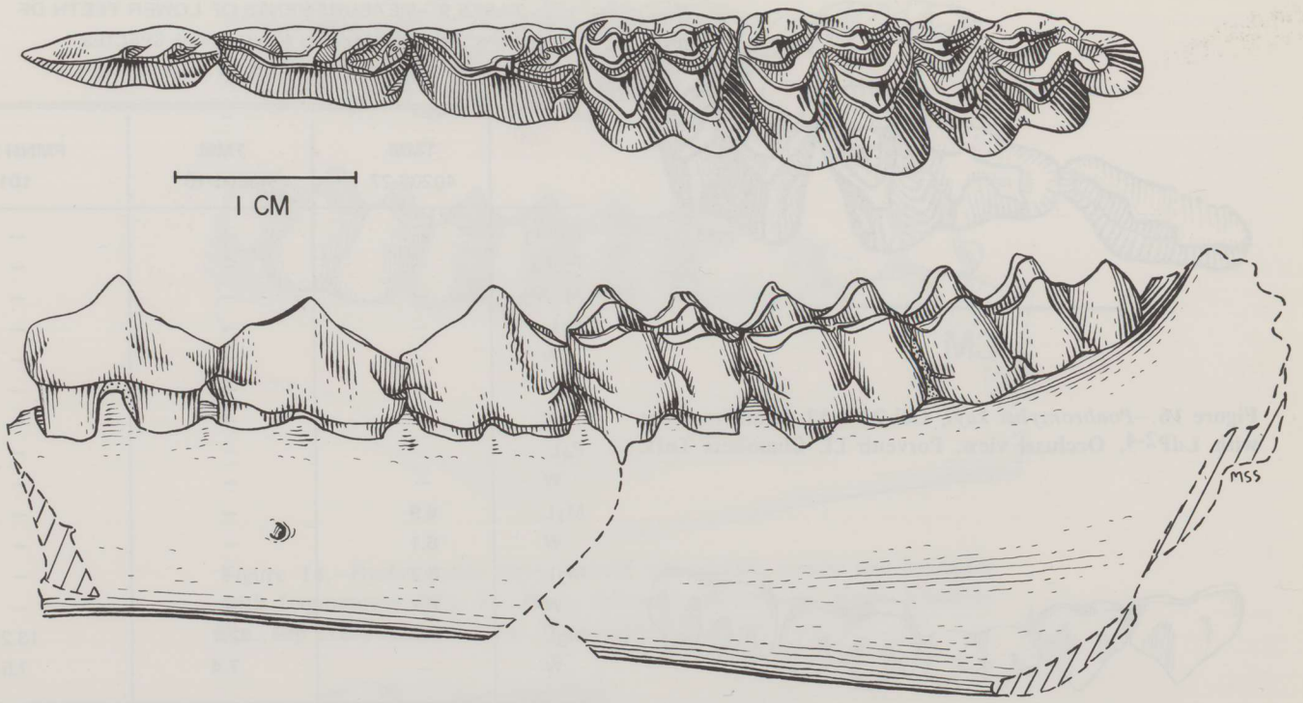


Figure 18.—*"Leptotragulus profectus,"* **FMNH PM 20766. Lower jaw fragment with P_{2-4}, M_{1-3}. Occlusal and external views. Chadron Fm., Peanut Peak Mem., Pennington Co., S. D.**

lower jaws with the second and third molars. The P_4 is narrow, elongate, without a metaconid, and with a narrow, V-shaped valley between the posterocristae. This same condition is found in *Leptotragulus proavus,* but that species, the genotype, is considerably smaller, enough so that *L. profectus* should very likely be referred to a new genus and species. Additional specimens with the same morphology on P_4 are now known from the Chadron Fm. of South Dakota. FMNH PM 20766 (fig. 18), a left ramus of a lower jaw with P_3-M_3 is from the Peanut Peak Member. Others are known from the Chadronian of Bates Hole, Wyoming. It is felt that it would be better to await the description of the Bates Hole material before assigning a new name. It is possible that some of the fragmentary specimens from the Porvenir l.f. of Texas may belong to this taxon rather than to *Poabromylus kayi.*

TABLE 10.—MEASUREMENTS OF LOWER TEETH OF *"LEPTOTRAGULUS PROFECTUS"* FROM NEBRASKA, SOUTH DAKOTA, AND WYOMING

	FMNH PM 20766 PP	FMNH PM 25893 PP	SDSM 5340 Y	TYPE *LEPTOTRAGULUS PROFECTUS* AMNH 9681 BH
P_2-M_3	62.6	–	–	–
P_2-P_4	29.9	–	24.0	24.6
M_1-M_3	33.2	–	–	–
P_2L	10.7	–	7.9	6.4
W	3.6	–	2.5	2.1
P_3L	10,8	–	8.5	9.3
W	4.3	–	3.4	3.2
P_4L	9.8	8.5	7.4	9.3
W	5.3	4.5	4.7	3.8
M_1L	9.3	9.6	–	–
W	7.7	7.8	–	–
M_2L	10.7	11.0	–	–
W	8.4	8.1	–	–
M_3L	14.1	15.6	–	–
W	7.8	7.5	–	–

Family Camelidae Gray, 1821
Subfamily Oromerycinae new subfamily

Gazin (1955) placed *Oromeryx, Protylopus, Camelodon, Malaquiferus,* and *Eotylopus* in a family Oromerycidae. The family is easily distinguished by the peculiar pattern of the protocone and the very distinctive lower molars. There is considerable question, however, whether all of the genera and species just listed belong in the family. For example, the teeth of *Camelodon arapahovius* are so worn that a pattern cannot be identified. Furthermore, the diastema between P_2 and P_3 would foreshadow that subfamily of camels in which such a tooth arrangement is characteristic, the Floridatragulinae (McKenna 1966; Maglio 1966; Patton 1966).

Protylopus petersoni Wortman, the genotypic species, also has teeth so worn as to be scarcely

identifiable, and the type of *Protylopus annectens* Peterson is lost. Gazin (1955) pointed out the possibility that *Oromeryx* and *Protylopus* might be synonymous but preferred to keep them separate.

Gazin (1955) did not place the small late Eocene *Poebrodon kayi* in the family Oromerycidae; instead, he made *Poebrodon* ancestral to *Poebrotherium* and placed it in the family Camelidae. Gazin must have been comparing *Poebrodon* with middle Oligocene specimens of *Poebrotherium;* and, to be sure, there is a similarity. However, Chadronian specimens of *Poebrotherium* show a closer relationship to *Protylopus* than they do to *Poebrodon.* The latter had already developed selenodont upper molars by the Uintan, whereas in Chadronian specimens of *Poebrotherium,* full selenodonty is only sporadically developed. For these reasons, I propose the new subfamily Oromerycinae within the family Camelidae.

In Wilson (1971a, pp. 35–36, 46) I presented evidence for the method of development of selenodonty in merycoidodonts from *Protoreodon.* The origin of selenodonty in poebrotheriines and oromerycines cannot be documented as fully because of a much smaller sample. Nonetheless, the number of poebrotheriines and oromerycines from the late Eocene/early Oligocene collections is sufficient to show that the selenodont upper molars in camelids were developed by a different method than that in merycoidodonts. Those Chadronian specimens of *Poebrotherium* that I have examined have, on the anterior molars, a diagonal loph that is directed posterointernally across the protocone and with a short loph projecting at right angles toward the median valley between the para- and metacones (figs. 25, 28). This bifurcate pattern is essentially the same pattern that is formed on all molars of *Protylopus* and *Eotylopus.*

The oromerycine pattern is similar to that described, but the posterointernal arm of the protocone is directed more posteroexternally, producing a more V-shaped structure (fig. 19.) In *Poebrotherium,* the posterointernal portion of the loph of the protocone is suppressed in the development of a protoselene whereas in the oromerycines a suppression of the median arm on the protocone would form a selenodont protocone.

If my interpretations are correct, selenodonty developed independently by different methods at different times during the late Eocene and early Oligocene.

Genus *Oromeryx* Marsh, 1894
Oromeryx sp.
Porvenir local fauna
Fig. 19; Table 11

Genotype.—Oromeryx plicatus Marsh, 1894. Right maxillary fragment with P^4 and the lingual portions of M^1-M^3; left maxillary fragment with M^3 and labial portion of M^2, YPM 14571.

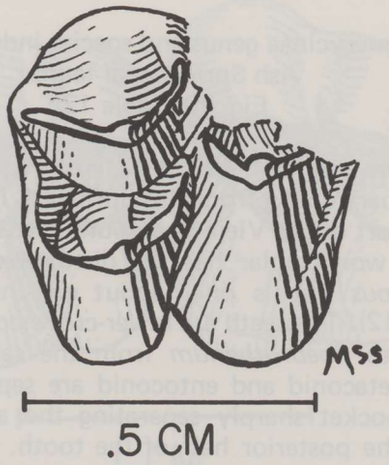


Figure 19.—*Oromeryx* sp. 40688-12. Upper molar fragment. Porvenir l.f., Chambers Tuff.

TABLE 11.—MEASUREMENTS OF UPPER TEETH OF OROMERYCINES FROM TEXAS, UTAH, AND WYOMING

	UINTA B AFTER GAZIN *OROMERYX PLICATUS* YPM 14571	*OROMERYX* SP. *40688-12* P	*MALAQUIFEROUS TOURTELOTI* USNM 20588 B	*CAST* CM 15392 TT
M^{1-3}	23.5		21.7	19.2
P^2 L				
W				
P^3 L				
W				
P^4 L			5.8	
W	5.7		6.5	
M^1 L	7.4@	?6.0@	6.8	6.7
W			7.8	6.5
M2L	8.3		7.4	7.4
W			8.8	8.0
M^3 L	8.8		7.5	7.0
W	9.3		9.0	7.8

Material.—One fragment of an upper molar, 40688-12.

Stratigraphic position.—Chambers Tuff Fm., approximately 200 feet above the Buckshot Ignimbrite. Porvenir l.f.

Age.—Early Chadronian.

Description.—A very small upper molar tooth fragment with paracone missing but with the very distinctive bifurcate protocone, can be referred with confidence to *Oromeryx.* The tooth is about 6 mm long and 6.2 mm wide across the hypocone-metacone. It is the size of a small *Leptomeryx.* The rib on the metacone is not as strong as in the molars of *Malaquiferus.* The mesostyle and meta-

style are not as pronounced as in *Leptomeryx.*

Oromerycinae genus and species indet., No. 1
Ash Spring local fauna
Fig. 20; Table 12

A jaw fragment, 40283-72, with P_4, M_2, and anterior part of M_3 from Ash Spring l.f. in the uppermost part of the Vieja Group undifferentiated. The partly worn molar has the distinctive pattern of *Eotylopus* but is only about one-third the size (table 12). The teeth are lower-crowned when compared to *Poebrotherium* from the same locality. The metaconid and entoconid are separated by a deep pocket sharply separating the anterior half from the posterior half of the tooth. Each half is almost circular in outline. The anterior portion of the P_4 is broken off, but the tooth is complete posterior to the main cusp. A small entoconid is present, which leads me to believe the tooth is a P_4 rather than a P_3.

This little oromerycid is about the size of what the lower tooth should be for *Malaquiferus,* but no lower teeth of that genus are known. It is between the sizes of *Protylopus petersoni* and *P. ?annectens* as given by Gazin (1955). More certain identification will have to await more material.

Oromerycinae genus and species indet., No. 2
Ash Spring local fauna
Fig. 21; Table 12

A lower molar tooth, 40283-25, Ash Spring l.f., is tentatively identified as an M_2. It is an oromerycid about half the size of *Eotylopus reedi* and larger than 40283-72. It is mentioned only to call attention to the presence of another of these rare forms in the collection.

Genus *Eotylopus* Matthew, 1910
Eotylopus cf. *reedi*
Little Egypt local fauna
Figs. 22, 23; Tables 13, 14

Type.—U. Wyo. V 316, a skull, jaws, and skeleton.

Referred material.—FMNH PM 13, left M_2; TMM 40840-7, left M^{2-3}; 40209-512, partial dP_4, M_{1-2}.

Stratigraphic position.—FMNH PM 13 is from the lower part of the Chambers Tuff about 200 feet above the Buckshot Ignimbrite; Porvenir l.f. TMM 40840-7 and 40209-512 are from the upper part of the Chambers Tuff within 10 feet below a pale red sandstone which is at the approximate position of the Bracks Rhyolite, Little Egypt l.f.

Age.—Chadronian.

Description.—The protocones of the two molar teeth 40840-7 have the very distinctive posterior bifurcation. A posterointernal projection from the protocone forms a straight line with an anteroexternal limb of the protoselene. This gives a T-shape to the protocone with the base of the T pointing posteroexternally (fig. 22). The enamel is rugose. On M^2 the ribs protrude farther externally than do the styles. The posterior rib on the metacone of M^3 has about the same external relief as the mesostyle and metastyle. The teeth are brachydont, and the paracone and metacone have a rounded, bunodont appearance because of the broad, rounded ribs. There is no external cingulum. Anterior and posterior cingula are present but do not connect across the internal margins of the hypocones. On M^3 the internal cingulum is continuous across the protocone. A median pillar is present between the protocone and the hypocone.

The single lower tooth, FMNH PM 13, is most probably an M_2. It is from a slightly larger individual than the upper teeth. The M_2 on TMM 40209-512 is difficult to measure because it is not fully erupted (fig. 23). As pointed out by Gazin (1955, p. 68), "the conical entoconid is distinctly isolated from the metaconid." The anterior crest of the protoconid is continued internally to connect with a prominent cusp (parastylid) anterior to the metaconid. It is similar in position to that described by Gazin (1955, p. 75) in *Protylopus ?annectens.* An anterior cingulum is present anterior to the parastylid. A short spur projects anteroexternally from the entoconid into the valley between the entoconid and metaconid. The posterior end of the posterior crest of the hypoconid is expanded to form a hypoconulid. A short median pillar is present between the protoconid and hypoconulid, but there is no external cingulum. There is no internal cingulum present. The enamel is slightly rugose.

Relationships.—*Eotylopus* and *Oromeryx,* the former relatively large and the latter small, survive into the Chadronian, retaining their primitive non-selenodont, low-crowned teeth. *Eotylopus* retains a short neck; postcranial elements for *Oromeryx* are unknown. The number of fragments of oromerycids in the Ash Spring l.f. of west Texas is surprising in view of their absence in Chadronian deposits farther north.

Subfamily Poebrotheriinae Zittel, 1893
Genus *Poebrotherium* Leidy, 1847
*Poebrotherium franki** new species
Airstrip and Ash Spring local faunas
Figs. 24-27; Tables 15, 16

Type.—TMM 40504-149, a skull with $I^{1-}M^3$, a lower jaw with P_2-M_1, and fragments of vertebrae.

Material.—TMM 40504-3, a cranial cast with bone fragments adhering and parts of M^{1-3}; —128, —191, palates with P^3-M^3; —187, a symphysis of a lower jaw with roots of I_{1-3}, C, P_{1-2}. All from Airstrip

*Named for Dr. R. M. Frank, who, as a student assistant, greatly aided in the collection and preparation of the Airstrip local fauna.

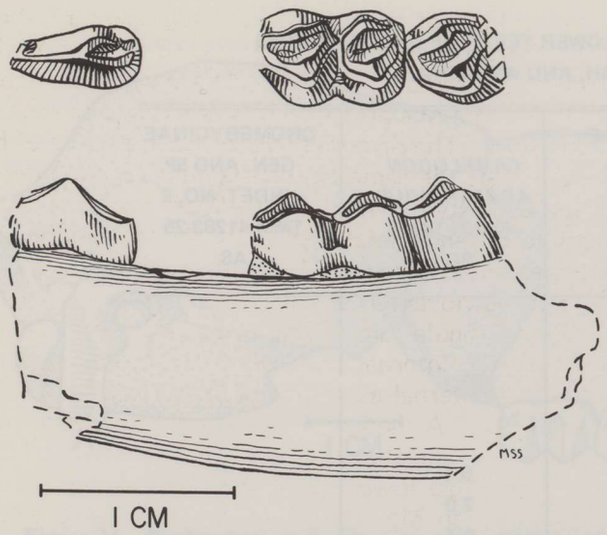


Figure 20.—Oromerycinae gen. and sp. indet. No. 1, 40283-72. Lower jaw fragment with P_4, M_2, and fragmentary M_3. Occlusal and external views. Ash Spring l.f., Vieja Gr. undifferentiated.

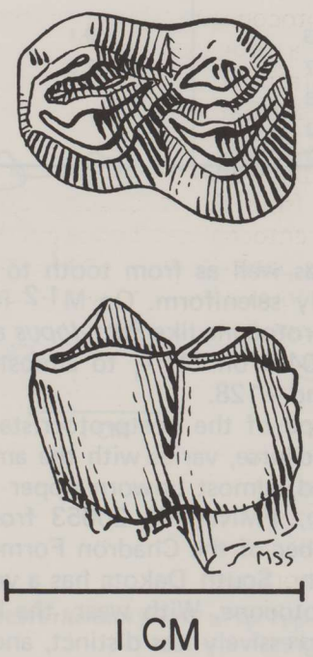


Figure 21.—Oromerycinae gen. and sp. indet No. 2, 40283-25. Lower molar tooth. Occlusal and external views. Ash Spring l.f., Vieja Gr. undifferentiated.

l.f. TMM 40203-85, M^{1-3}; –90, M^{2-3}; –88, M_{1-3}; –84, fragmentary P_2, P_3, fragmentary P^4 and M_1 and M_3; –30, dP^4; –62, M_1 and fragmentary M_3; all from Ash Spring l.f.

Stratigraphic position.—Capote Mt. Tuff, approximately 570 feet above Bracks Rhyolite, Airstrip l.f. Vieja Group undif., Ash Spring l.f.

Age.—Chadronian.

Diagnosis.—A very small poebrothere with a bifurcate protoselene on one or more of the molars.

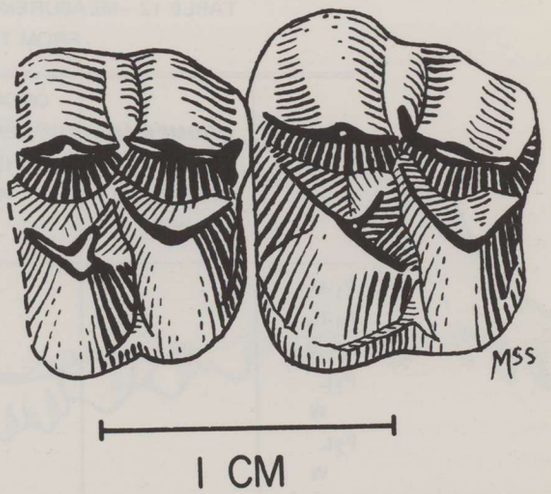


Figure 22.—*Eotylopus* cf. *reedi*, 40840-7. Skull fragment with LM^{2-3}. Occlusal view. Little Egypt l.f., Chambers Tuff.

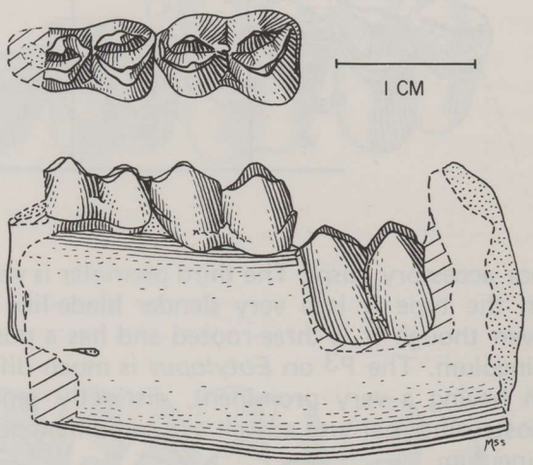


Figure 23.—*Eotylopus* cf. *reedi*, 40209-512. Lower jaw fragment with M_1, M_{2-3}. Occlusal and external views. Little Egypt l.f., Chambers Tuff.

Elongate snout with I^{2-3} aligned anteroposteriorly. Canine small but slightly larger than I^3. P^3 three-rooted but with no internal cusp and with or without internal cingulum. Molars with or without median pillar. P_2 is a simple blade, P_3 and P_4 each have an internal crista. No entoconid on P_4.

Description.—The upper dentition (figs. 24, 25) is complete on the left side of TMM 40504-149. The individual was young; M^3 is completely erupted but unworn. I^1 is oriented with its long axis at right angles to the length of the jaw. I^{2-3} and the canine have their long axes more or less parallel with the length of the jaw, and each has an anterior and posterior cutting edge. The first premolar is a two-rooted, simple elongate blade with a very small anterior swelling in the position of the paracone. P^2 is also trenchant but is gently curved. There is a more pronounced paracone on P^2 but no cingular

TABLE 12.–MEASUREMENTS OF LOWER TEETH OF OROMERYCINES FROM TEXAS, UTAH, AND WYOMING

	OROMERYX PLICATUS USNM 20391 WRU	OROMERYCINAE GEN. AND SP. INDET. NO. 1 40283-72 AS	*CAMELODON ARAPAHOVIUS* AMNH 14604 BD	OROMERYCINAE GEN. AND SP. INDET. NO. 2 TMM 41283-25 AS
P_1-M_3				
P_1-P_4				
M_1-M_3	26.1		27.1	
P_1L				
W				
P_2L			6.4	
W			2.0	
P_3L			6.7	
W			2.3	
P_4L		6.5	7.0	
W		2.8	2.9	
M_1L	7.0		6.8	
w	4.7			
M_2L	7.9	7.8	8.3	9.1
W	5.6	4.7	5.7	7.5
M_3L	11.2		12.8	
W	5.7@	5.8	5.3	

nor accessory cusps. The third premolar is variable. In the type it is a very slender blade-like tooth even though it is three-rooted and has a posterior cingulum. The P^3 on *Eotylopus* is much different in having a very prominent, distinctly separated posterointernal cusp as well as a prominent posterocingulum.

The P^4s on the available specimens show some variation. The internal selene is sharply set off from the outer cusp and is slightly forward of and smaller than the outer cusp. That is, the inner half of the P^4 seems pinched when compared to the outer half. On the P^4s of the type there is a ridge that connects the posterior cingulum to the posterior arm of the selene, thereby forming a pocket at the posterointernal corner of the tooth. On –191 such a ridge is present on the right P^4 but not on the left. On the latter, a short ridge of enamel divides the fossette into two unequal parts; the smaller is anterior. The premolars of *P. franki* are higher-crowned, have thinner enamel, and are more widely spaced than the premolars of *E. reedi.*

The molar teeth are moderately high-crowned for the size of the individuals. The para- and metastyles are prominent, as are the ribs. A small median pillar may or may not be present. The para- and metacones are shorter anteroposteriorly and thinner than the same cusps on *E. reedi.* The hypocone is always seleniform, but the protocone shows considerable variation from specimen to specimen as well as from tooth to tooth. On M^3 it is usually seleniform. On M^{1-2} it varies from a bifurcate protocone like *Protylopus* and *Eotylopus,* as in 40504-3 on M^{1-2}, to almost seleniform in the type and –128.

The shape of the postprotocrista of the protoselene, of course, varies with the amount of wear. An isolated, almost unworn upper molar of *Poebrotherium,* FMNH PM 20053 from the Peanut Peak Member of the Chadron Formation of Shannon County, South Dakota has a very distinct bifurcate protocone. With wear, the bifurcation becomes progressively less distinct, and the posterior arm of the protoselene takes on a swollen appearance.

The outer surface of the nodules that contained skulls of *P. franki* are weathered, and for that reason it is impossible to describe the skull structure in detail. There appears to have been a lacrimal vacuity. The dorsal part of the maxillary is depressed so that the muzzle must have been narrow even though the type is slightly crushed. On the right side there is enough of the ear region preserved to be certain that the bullae were enlarged.

A fragment of the left lower jaw contains P_{2-4}, M_1 (fig. 26). The P_2 is a simple blade; P_3 and P_4 have small paracones. On P_3 the posterocrisdid divides into two closely parallel ridges. There are no accessory cusps on the posterior margin of P_3. The posterior part of P_4 is broken, but the an-

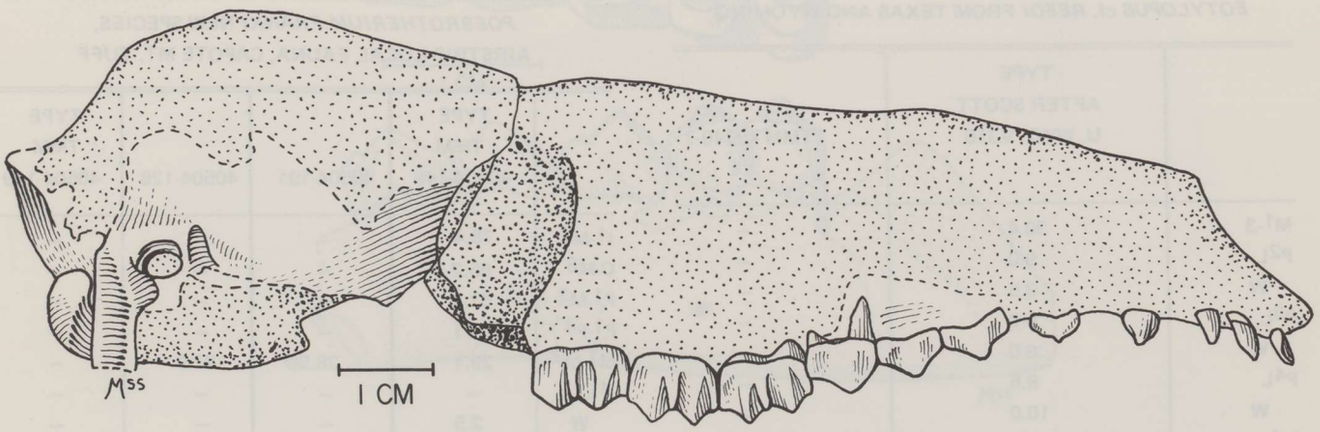


Figure 24.—*Poebrotherium franki* n. sp. type, 40504-149. Fragmentary skull, right side. Airstrip l.f., Capote Mt. Tuff.

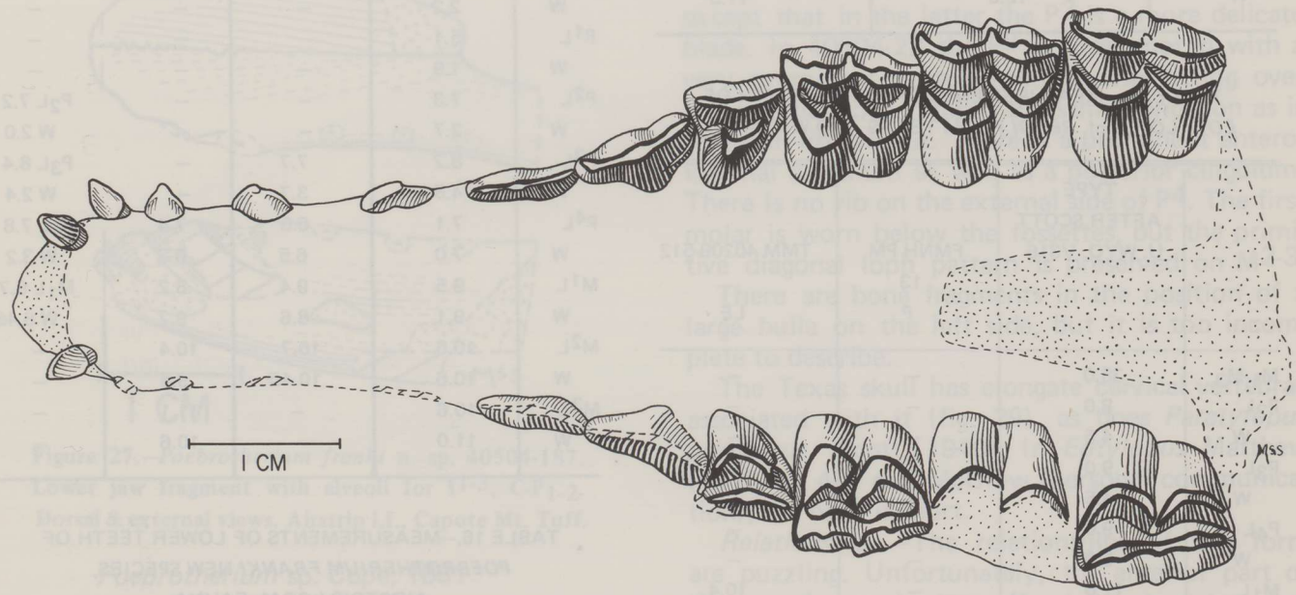


Figure 25.—*Poebrotherium franki* n. sp. type, 40504-149. Fragmentary skull, palatal view. Airstrip l.f., Capote Mt. Tuff.

terior part is like P_3, only the tooth is larger. M_1 has no median pillar and no external cingulae. The arrangement of the anterior teeth in the lower jaw is shown in a fragment of 40504-187 (fig. 27).

Relationships.—The origins of the Camelidae have been discussed at length by many authors. *Poebrotherium* from the middle Oligocene Brule Formation has been variously placed taxonomically but generally conceded to be an early member of the line leading to the true camels. *Eotylopus* was known from the early Oligocene of Wyoming, but to my knowledge no specimens of *Poebrotherium* have been previously described from the early Oligocene or Chadronian, although some have apparently rested in museum trays for a number of years. Scott (1937, 1940) pointed out the similarities of *Eotylopus* and the late Eocene *Protylopus,* and Gazin (1955) placed these two genera together with *Oromeryx, Camelodon,* and *Malaquiferus* in a new family, the Oromerycidae. In the same paper, Gazin (1955) described the new genus *Poebrodon* from late Eocene Uinta C and considered it to be directly ancestral to *Poebrotherium* and stated (Gazin, 1955, p. 79), " . . . *Poebrodon* is scarcely more than a very small *Poebrotherium.*" On page 81, Gazin (1955) remarks on "the precocious *Poebrotherium* -- like molars of *Poebrodon.* Here the selenodonty is advanced but of a different character, in which an early union is established between the crests of the inner and outer cusps."

As stated earlier, the upper molar teeth of *Poebrodon* do indeed resemble an Orellan *Poebrotherium.* On the type of *Poebrodon,* the only known specimen, M^1 is badly worn and wear

TABLE 13.–MEASUREMENTS OF UPPER TEETH OF *EOTYLOPUS* cf. *REEDI* FROM TEXAS AND WYOMING

	TYPE AFTER SCOTT U. WYO. V316	TMM 40840-7 LE
M^{1-3}	30.4	–
P^2L	9.0	–
W	3.5	–
P^3L	9.0	–
W	6.0	–
P^4L	8.5	–
W	10.0	–
M^1L	7.5	–
W	11.0	–
M^2L	11.0	8.3
W	13.0	10.5
M^3L	12.0	9.8
W	12.5	11.5

TABLE 14.–MEASUREMENTS OF LOWER TEETH OF *EOTYLOPUS* cf. *REEDI* FROM TEXAS AND WYOMING

	TYPE AFTER SCOTT U. WYO. V316	FMNH PM 13 P	TMM 40209-512 LE
M_{1-3}	38.0	–	–
P_2L	8.0	–	–
W	4.5	–	–
P_3L	9.0	–	–
W	4.5	–	–
P_4L	9.0	–	–
W	5.0	–	–
M_1L	11.0	–	10.4
W	7.0	–	6.8
M_2L	11.0	11.4	11.2@
W	8.5	9.7	8.1
M_3L	17.0	–	–
W	9.0	–	–

TABLE 15.–MEASUREMENTS OF UPPER TEETH OF *POEBROTHERIUM FRANKI* NEW SPECIES, AIRSTRIP LOCAL FAUNA, CAPOTE MT. TUFF

	TYPE TMM 40504-149	40504-191	40504-128	TYPE TMM 40504-149
I^{1-M^3}	78.4	–	–	–
$C-M^3$	65.2	–	–	–
P^{1-M^3}	57.8	–	–	–
P^{1-P^4}	30.1	–	–	–
M^{1-M^3}	29.1	28.9@	27.9	–
I^1L	–	–	–	–
W	2.5	–	–	–
I^2L	2.7	–	–	–
W	1.8	–	–	–
I^3L	2.8	–	–	–
W	1.9	–	–	–
CL	3.2	–	–	–
W	2.2	–	–	–
P^1L	5.1	–	–	–
W	1.9	–	–	–
P^2L	7.3	–	–	P_2L 7.2
W	2.7	–	–	W 2.0
P^3L	8.2	7.7	–	P_3L 8.4
W	4.5	3.7	–	W 2.4
P^4L	7.1	6.5	7.4	P_4L 7.8
W	7.0	6.5	6.8	W 3.2
M^1L	9.5	9.4	8.2	M_1L 9.7
W	9.1	8.6	9.2	W 6.4@
M^2L	10.6	10.7	10.4	–
W	10.6	10.4@	9.8	–
M^3L	10.6	–	11.1	–
W	11.0	–	10.6	–

TABLE 16.–MEASUREMENTS OF LOWER TEETH OF *POEBROTHERIUM FRANKI* NEW SPECIES, AIRSTRIP LOCAL FAUNA

	TMM 40504-149
P_2-P4	22.1@
P_2L	7.2
W	2.0
P_3L	7.9
W	2.4
P_4L	8.1@
W	3.3@
M_1L	9.7@
W	6.5@

on M^2 and M^3 is advanced to the point that it is impossible to be certain that the unworn protocone was not bifurcate. Until more material of *Poebrodon* is found, I am not convinced that it is ancestral to *Poebrotherium.* The bifurcate protocone on one or more molars of the early Oligocene *Poebrotherium* seems to preclude this. An alternative, to be sure, would be to refer those forms with bifurcate protocones to *Eotylopus.* There is, I believe, a preponderance of characters such as elongation of the snout, spaced premolars, higher crowns, similar P^3 pattern that weigh in favor of *Poebrotherium.* This would mean that *Protylopus* of the late Eocene could well be a common ancestor for both *Eotylopus* and *Poebrotherium.*

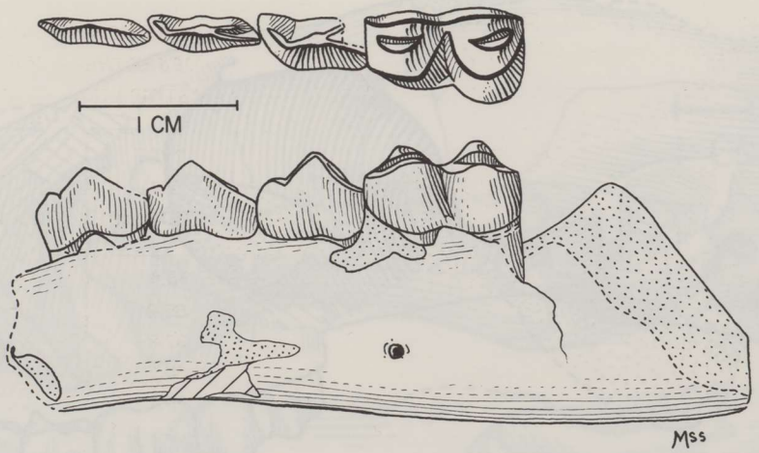


Figure 26.—*Poebrotherium franki* **n. sp. type, 40504-149. Lower jaw fragment with P_{2-4}, M_1. Occlusal and external views. Airstrip l.f., Capote Mt. Tuff.**

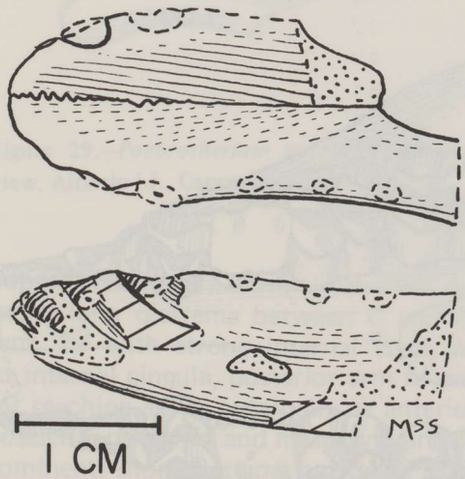


Figure 27.—*Poebrotherium franki* **n. sp. 40504-187. Lower jaw fragment with alveoli for I^{1-3}, C-P_{1-2}. Dorsal & external views. Airstrip l.f., Capote Mt. Tuff.**

Poebrotherium sp. Cope, 1881
Airstrip local fauna
Figs. 28-30; Tables 17, 18

Material.—TMM 40504-22, a skull with P^2, M^3, atlas, axis, and cervical vertebrae 3, 4, 5 and fragments of 6, proximal ends of metacarpals III and IV; —141, a fragmentary lower jaw with impression of P_1-M_3.

Stratigraphic position.—Capote Mt. Tuff approximately 570 feet above Bracks Rhyolite.

Age.—Chadronian.

Description.—The skull and cervical vertebrae, TMM 40504-22 from the Airstrip local fauna, are from a larger animal than *Poebrotherium franki.* The upper molar teeth (fig. 28) are worn, and the bifurcate protocone is present only in M^3. The molars are low-crowned, squat, and with thick rugose enamel. The ribs and styles are prominent. The P^2 is a simple blade with the main cusp slightly anterior to the middle of the tooth. It is similar to the P^2 in the contemporary small *Poebrotherium* except that in the latter the P^2 is a more delicate blade. In 40504-22 the P^3 is three-rooted with a very prominent posterointernal cusp sitting over the internal root. This is the same condition as is found in *Protylopus.* There is a prominent anterointernal cingulum as well as a posterior cingulum. There is no rib on the external side of P^4. The first molar is worn below the fossettes, but the primitive diagonal loph pattern is preserved on M^{2-3}.

There are bone fragments in the position of a large bulla on the left side, but it is too incomplete to describe.

The Texas skull has elongate cervical vertebrae associated with it (fig. 29), as does *Paratylopus primaevus* (Scott, 1940). In *Eotylopus* Matthew (1910, p. 40) and McGrew (personal communication), the neck is short.

Relationships.—The relationships of this form are puzzling. Unfortunately, the anterior part of the muzzle was broken off prior to burial so that the arrangement of the incisors and canines could not be seen. If I am correct in assigning the lower jaw 40504-151 to this taxon, whatever it may turn out to be, the anterior teeth were not spaced. The impression of the first premolar and the root of the canine are close to the second premolar. There is no diastema, as one might expect if this form were related to *Paratylopus.* But on the other hand, a Chadronian *Paratylopus* is not known. The premolars in both the skull and lower jaw from Texas are elongate, a character which is more like *Poebrotherium* than *Paratylopus.* The elongate cervical vertebrae eliminate this form from any relationship to *Eotylopus.*

Scott (1940) makes much of a contrast between the larger, sturdier *P. labiatum* and the slender, more delicate *P. wilsoni.* It may be that in the Airstrip local fauna there are representatives showing the same condition. *P. franki* is sufficiently dis-

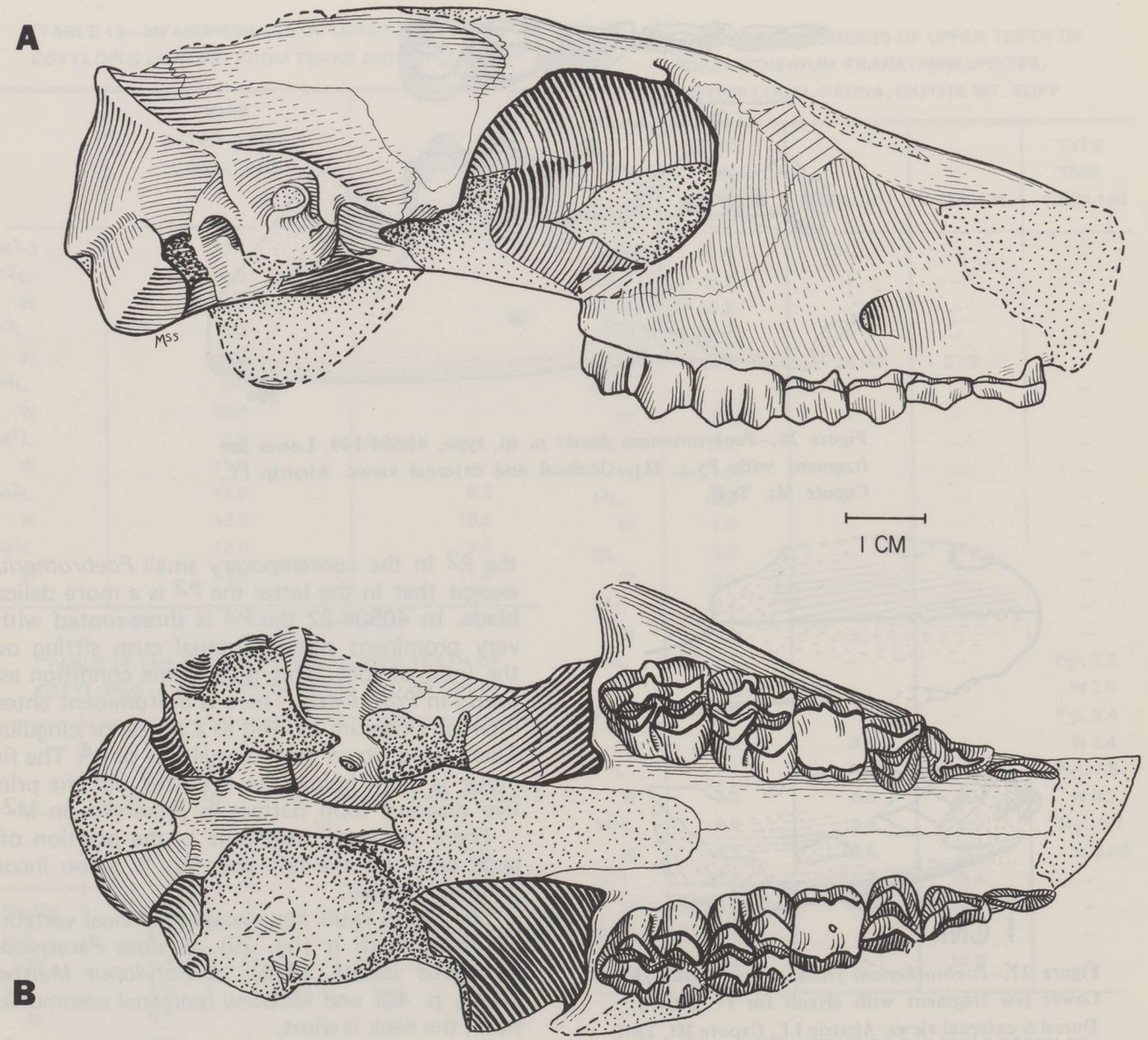


Figure 28.—*Poebrotherium* **sp. 40504-22. Fragmentary skull.** *A.* **Lateral view.** *B.* **Palatal view. Airstrip l.f., Capote Mt. Tuff.**

tinct from *P. wilsoni* to warrant a new species, but I prefer to wait until more is known of the variation in species of *Poebrotherium.*

Subfamily Poebrodoninae new subfamily

This subfamily is proposed to group *Poebrodon* and the new genus *Hidrosotherium.* I have already stated my reasons (p. 24) for differing with Gazin's (1955) interpretation that *Poebrodon* is ancestral to *Poebrotherium.* With the discovery of *Hidrosotherium,* described below, there is now a separate line of advanced camelids that appear as early as Uinta C. On figure 4 I have shown this subfamily converging with the subfamily Poebrotheriinae. Certainly more data is needed to confirm or deny this interpretation, which resembles interpretations found within the Order Primates where authors try to place extinct families under Suborders based on Recent forms.

Genus *Hidrosotherium* * new genus

Stratigraphic position.—Lower part of Chambers Tuff, Presidio Co., Texas.

Generic characters.—A small, delicate camelid,

**Hidros,* Gr. "perspiration;" *therium,* "animal." In reference to the sweat spent in collecting, preparing the specimen from the hard matrix, and in classifying the beast.

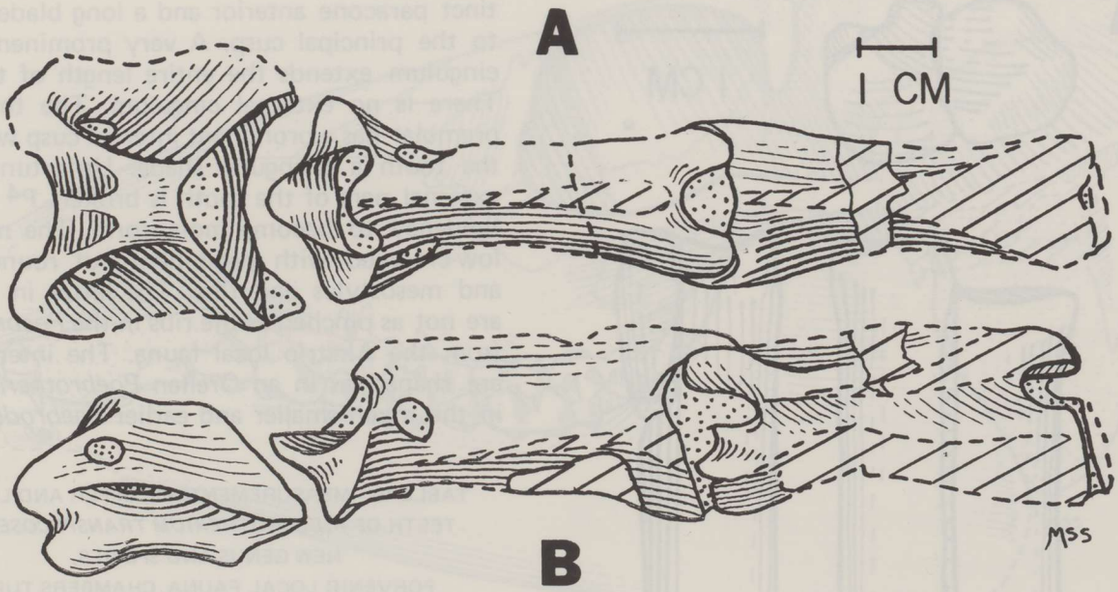


Figure 29.—*Poebrotherium* **sp. 40504-22. Atlas, axis, and first cervical vertebra.** *A.* **Dorsal view.** *B.* **Lateral view. Airstrip l.f., Capote Mt. Tuff.**

orbits open posteriorly, lacrimal vacuities present, P^1 absent, long diastema between C and P^2, P^2 trenchant, P^3 with strong internal cusp, molars without internal cingula, posterior arm of protoselene not reaching as far externally as anterior arm of hyposelene, parastyle and mesostyle prominent, ribs prominent, short diastema between P_1 and P_2, lower molars sharply selenodont, P_2 without opposing tooth.

*Hidrosotherium transpecosensis** n. gen. and sp.
Porvenir local fauna
Figs. 31-33; Table 19

Type.—FMNH PM 454, articulated skull and jaws with P^2-M^3, P_1-M_3. Chambers Tuff, Blue Cliff Horizon, 3/4 miles NNE of Big Cliff, Presidio Co., Texas.

Material.—FMNH PM 453, posterior part of skull with worn P^3-M^3. Same locality as type.

Stratigraphic position.—The Field Museum specimens were collected from the "Blue Cliffs" horizon. From the field notes loaned to me by Professor Bryan Patterson, this horizon is approximately 200 feet above the Buckshot Ignimbrite and is in the lower part of the Chambers Tuff, Porvenir l.f.

Age.—Early Chadronian.

Diagnosis.—Small artiodactyl, probably with reduced upper incisors, upper first premolar questionably absent, molars brachydont, selenodont,

*Geographic locality: Trans-Pecos Texas

TABLE 17.—MEASUREMENTS OF UPPER TEETH OF *POEBROTHERIUM* SP., AIRSTRIP LOCAL FAUNA, CAPOTE MT. TUFF.

	TMM 40504-22
M^1-M^3	34.4
P^2L	10.4
W	3.0
P^3L	9.4
W	7.1
P^4L	8.4
W	9.3
M^1L	10.2
W	10.9
M^2L	12.7
W	12.6
M^3L	13.3
W	13.4

TABLE 18.—MEASUREMENTS OF CERVICAL VERTEBRAE OF *POEBROTHERIUM* SP., AIRSTRIP LOCAL FAUNA

TMM 40504-22	
Atlas, anterior-posterior dorsal midline	17.9
Axis, anterior-posterior ventral midline	58.7
Cerv. 1, anterior-posterior ventral midline	52.0

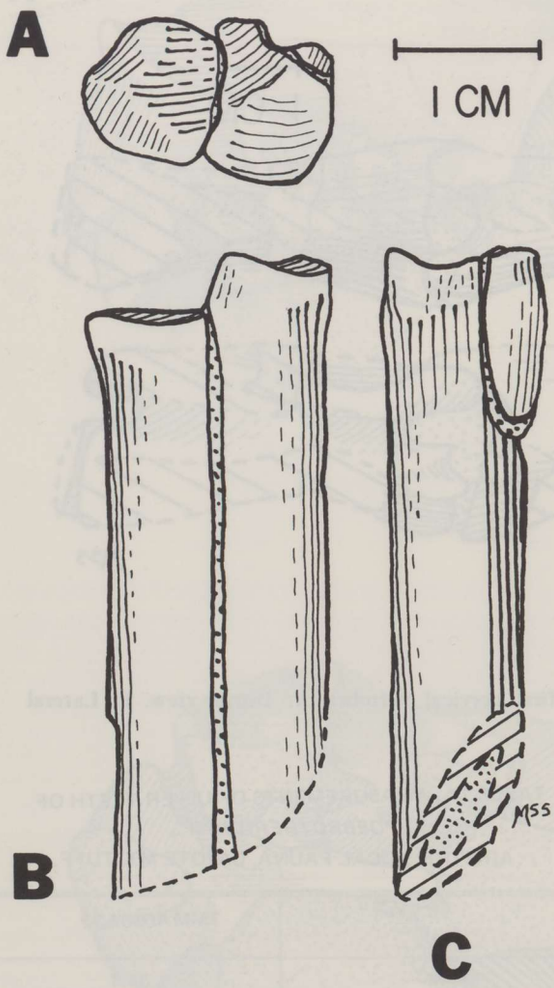


Figure 30.—*Poebrotherium* **sp. 40504-22. Proximal ends of metacarpals III and IV.** *A.* **Proximal view.** *B.* **Anterior view.** *C.* **Lateral view. Airstrip l.f., Capote Mt. Tuff.**

with strong styles and ribs, no internal cingulum or median pillar, lower first premolar elongate with posterior cusp and single-rooted, P_4 apparently without metaconid, preorbital fossae present, no large cancellous bullae.

Description.—The type (fig. 31) is an almost complete skull and jaws preserved in very hard matrix -- so hard that it is impossible to separate one from the other in order to get a full view of the occlusal surfaces of the teeth. Enough can be seen of the teeth on the right side to establish its affinities with the camels. The skull and jaws resemble *Leptomeryx,* but the dentition is entirely different.

The anterior part of the snout is missing so that the arrangement of the incisor teeth is uncertain, but it would appear that if incisors were present, they were reduced. An alveolus is present in what appears to be the anterior-most part of the maxillary and is assumed to be for the canine. A long diastema (19.3 mm in the type) separates this alveolus from the anterior part of P^2. The second upper premolar (fig. 32) is a long, narrow tooth. Although the tooth is damaged, the principal cusp does not appear to have been high. There is a distinct paracone anterior and a long blade posterior to the principal cusp. A very prominent internal cingulum extends the entire length of the tooth. There is no external cingulum. The third upper premolar has a prominent internal cusp which gives the tooth a triangular shape. Unfortunately, the external part of the tooth is broken. P^4 shows no tendency to become molariform. The molars are low-crowned with prominent but rounded para- and mesostyles and ribs. The latter in particular are not as pinched as the ribs in the *Poebrotherium* from the Airstrip local fauna. The internal cusps are shaped as in an Orellan *Poebrotherium* or as in the much smaller and earlier *Poebrodon.* There

TABLE 19.—MEASUREMENTS OF UPPER AND LOWER TEETH OF *HIDROSOTHERIUM TRANSPECOSENSIS* NEW GENUS AND SPECIES, PORVENIR LOCAL FAUNA, CHAMBERS TUFF.

	TYPE CNMH PM 454
$\underline{C}nP^1$-M^3	62.0@
P^2-M^3	39.4
M^1-M^3	22.5
P^2L	6.8
W	2.8
P^3L	6.5@
W	–
P^4L	6.6
W	–
M^1L	6.3
W	–
M^2L	7.6
W	–
M^3L	8.2
W	–
P_1-M_3	54.6@
P_2-M_3	43.7@
M_1-M_3	26.2@
P_1L	3.4
W	–
P_2L	5.5@
W	–
P_3L	6.0
W	–
P_4L	6.6
W	–
M_1L	7.2
W	–
M_2L	7.8@
W	–
M_3L	10.5@
W	–

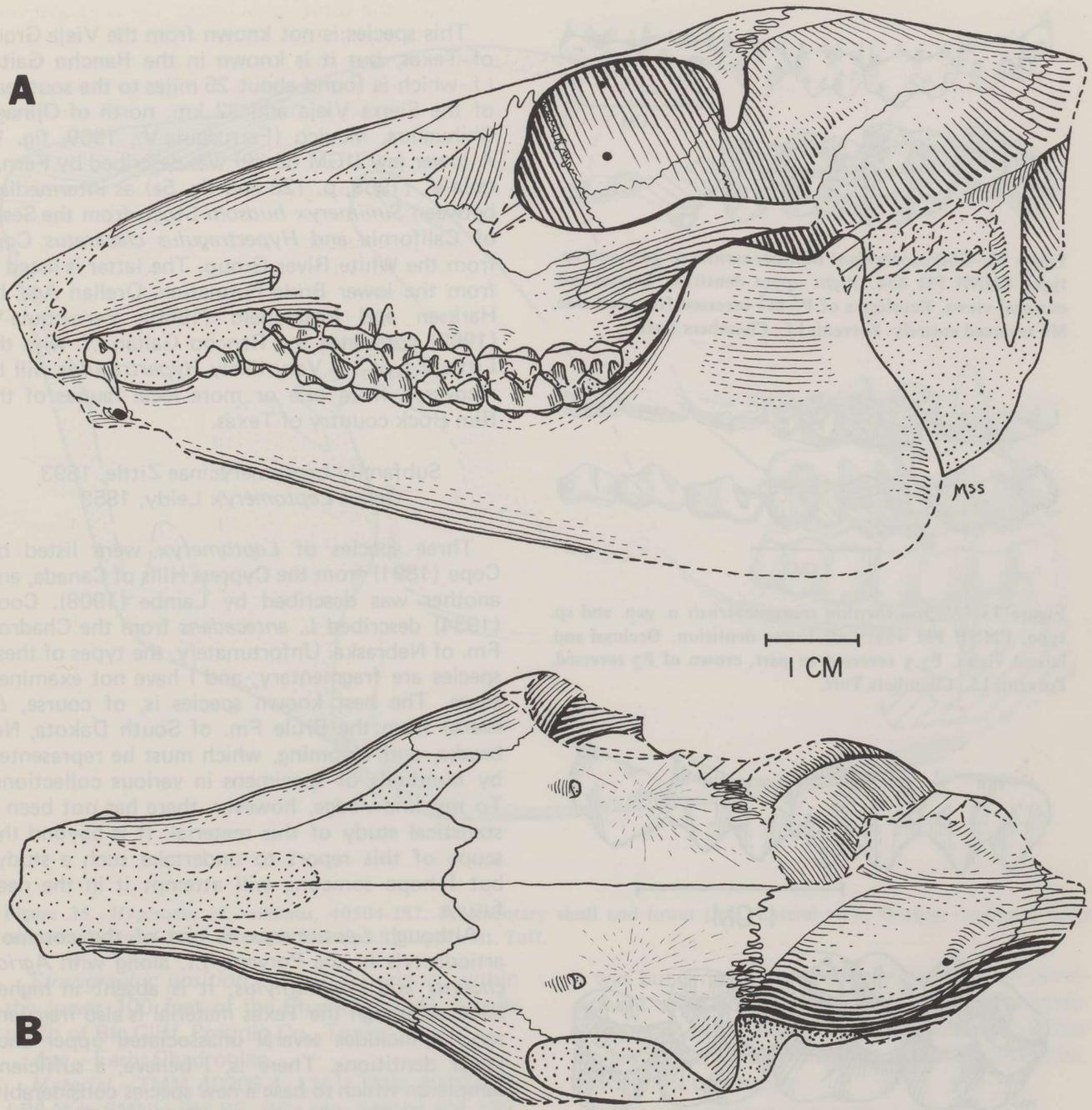
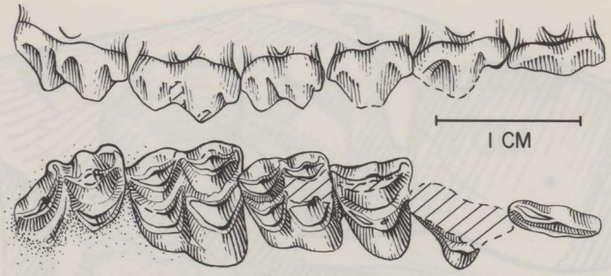


Figure 31.—*Hidrosotherium transpecosensis* **n. gen. and sp. type, FMNH PM 454. Articulated skull and jaws.** *A.* **Lateral view.** *B.* **Dorsal view. Porvenir l.f., Chambers Tuff.**

are no median pillars and only an anterior cingulum on the external half of the tooth.

The anterior part of the lower jaw is also broken, but a large alveolus is preserved, presumably for the canine. The first lower premolar (fig. 31) is single-rooted, somewhat elongate, with a small posterior cusp. P_2 is trenchant, with small cusps anterior and posterior to the main cusp. The internal portions of the lower premolars and molars (fig. 33) are not visible. The paracone on P_3 is turned sharply internally, but it is not rounded. The posterior part of P_3 is open; a metaconid is probably present, at least a ridge extends from a cuspid that is posterior and separate from the main cusp to the posteroexternal corner of the tooth. A very small cuspule is present at the posterointernal corner of the tooth. Almost the same description applies to P_4 except that there does not seem to be a metaconid. The posterior part of the tooth is open, and there is a small posterointernal cuspulid. Enough of the lower molars were exposed to show the external selenes.

Relationships.—The relationships of this form are puzzling. The general appearance of the skull resembles a large *Leptomeryx,* but the premolar and molar tooth patterns in no way resemble that genus. The molar teeth resemble a middle Oligocene *Poebrotherium,* but premolars are protocera-



Figire 32.—*Hidrosotherium transpecosensis* n. gen. and sp. type, FMNH PM 454. Right upper dentition. Lateral and occlusal views. Ectolophs of P^3-M^3 reversed from left side, M^3 reversed entirely. Porvenir l.f., Chambers Tuff.

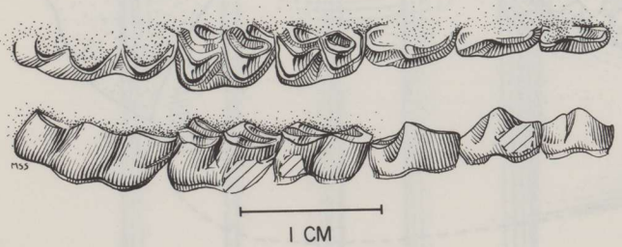


Figure 33.—*Hidrosotherium transpecosensis* n. gen. and sp. type, FMNH PM 454. Left lower dentition. Occlusal and lateral views. P_{2-3} reversed in part, crown of P_2 reversed. Porvenir l.f., Chambers Tuff.

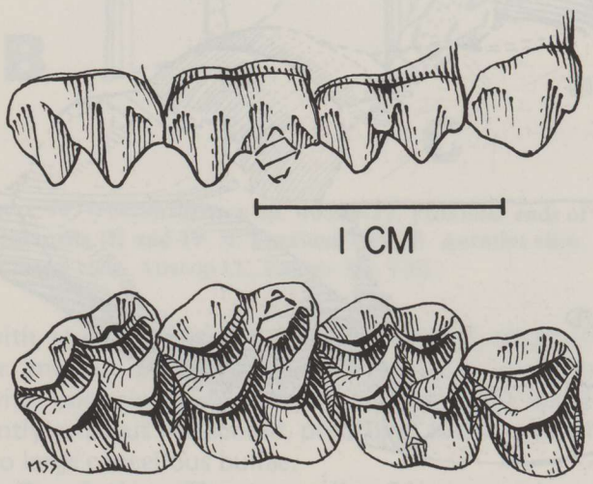


Figure 34.—*Leptomeryx defordi* n. sp. type, FMNH PM 58. Skull fragment with P^4-M^3. Lateral and occlusal views. Porvenir l.f., Chambers Tuff.

tid. I tentatively ally *Hidrosotherium* with the camelids and believe it represents a line evolving from *Poebrodon* parallel with lines leading from *Protylopus* to *Poebrotherium* and from *Protylopus* to *Eotylopus,* although *Eotylopus* may well have come from *Oromeryx.*

Suborder Ruminantia Scopali, 1777
Infraorder Tragulina Flower, 1883
Superfamily Hypertraguloidea Scott, 1940
Family Hypertragulidae Cope, 1879
Hypertragulus heikeni Ferrusquia-V, 1969

This species is not known from the Vieja Group of Texas, but it is known in the Rancho Gaitan l.f. which is found about 25 miles to the southeast of the Sierra Vieja and 32 km. north of Ojinaga, Chihuahua, Mexico (Ferrusquia-V., 1969, fig. 1). A lower jaw (IGM 65-39) was described by Ferrusquia-V. (1969, p. 128 and fig. 5e) as intermediate between *Simimeryx hudsoni* Stock from the Sespe of California and *Hypertragulus clacaratus* Cope from the White River Group. The latter is listed as from the lower Brule Formation, Orellan Age, by Harksen and Macdonald (1969). Ferrusquia-V. (1969) correlates the Rancho Gaitan l.f. with the Little Egypt l.f. Very likely *Hypertragulus* will be recovered from one or more local faunas of the Rim Rock country of Texas.

Subfamily Leptomerycinae Zittle, 1893
Genus *Leptomeryx* Leidy, 1853

Three species of *Leptomeryx* were listed by Cope (1891) from the Cypress Hills of Canada, and another was described by Lambe (1908). Cook (1934) described *L. antecedens* from the Chadron Fm. of Nebraska. Unfortunately, the types of these species are fragmentary, and I have not examined them. The best known species is, of course, *L. evansi* from the Brule Fm. of South Dakota, Nebraska, and Wyoming, which must be represented by hundreds of specimens in various collections. To my knowledge, however, there has not been a statistical study of this material. It is beyond the scope of this report to undertake such a study, but I hope someone will attempt it in the near future.

Although *Leptomeryx* is one of the common artiodactyls in the Porvenir l.f. along with *Agriochoerus* and *Poabromylus,* it is absent in higher beds. Although the Texas material is also fragmentary, it includes several unassociated upper and lower dentitions. There is, I believe, a sufficient sample on which to base a new species considerably more primitive than *L. evansi.* In the Texas species, the protoselene is not fully developed in five of the six specimens with one or more upper molar teeth. In contrast, examination of 30 upper dentitions from the Brule Fm. at the U. S. National Museum reveals only three teeth, either M^1 or M^2 with an undeveloped protoselene.

*Leptomeryx defordi** new species
Porvenir local fauna
Fig. 34; Tables 20, 21

Type.—FMNH PM 58, right maxillary fragment with P^4-M^3.

*Named for Ronald K. DeFord, Professor of Geology, The University of Texas at Austin and supervisor of geologic mapping in the Vieja area during the 1950s and 1960s.

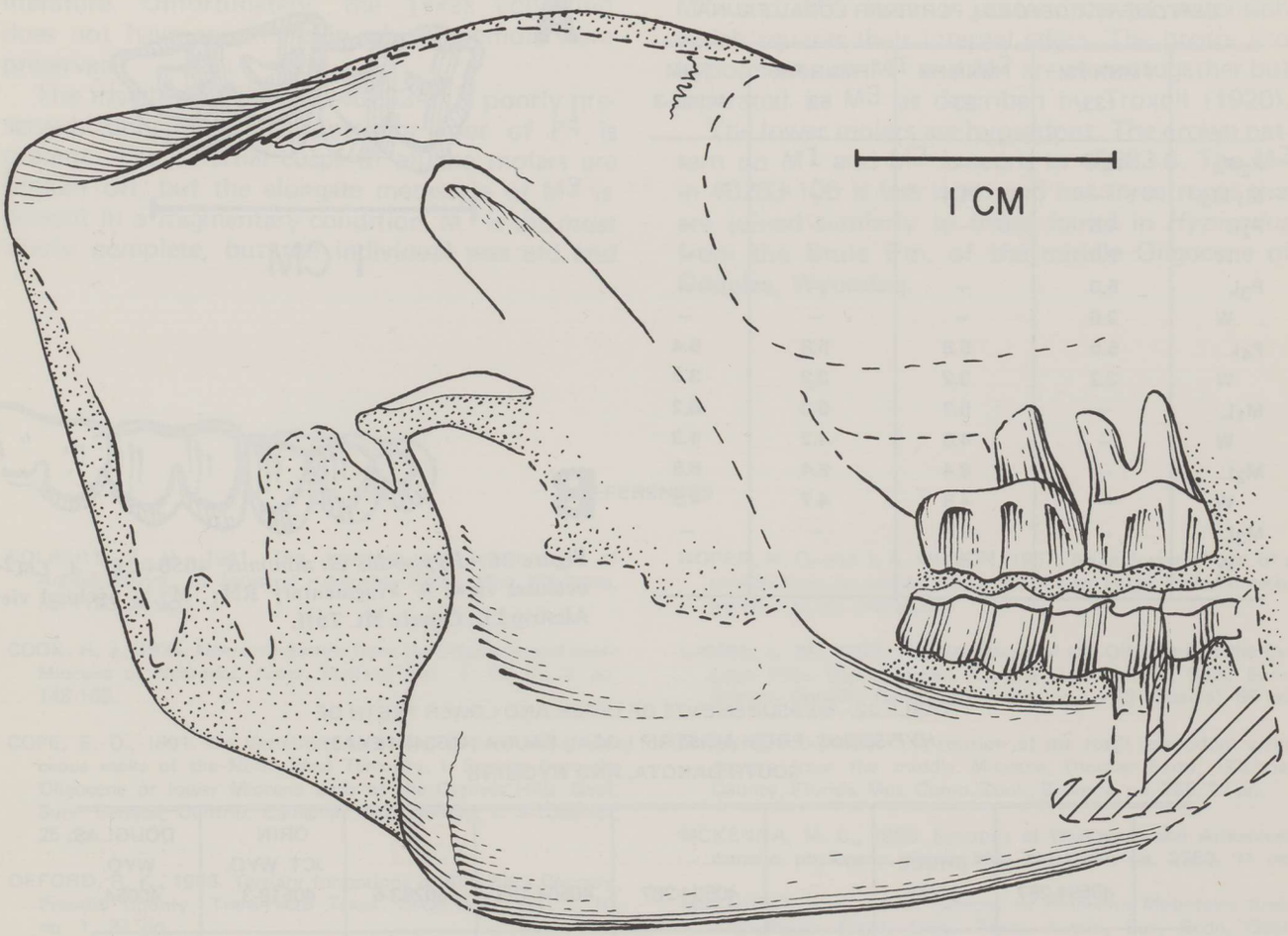


Figure 35.—*Hypisodus* cf. *minimus*, **40504-287. Fragmentary skull and lower jaws. Lateral view. Occiput reversed, orbit and lateral view of M^{2-3} reversed. Airstrip l.f., Capote Mt. Tuff.**

Stratigraphic position.—Big Red horizon, within the lower 100 feet of the Chambers Tuff, ¼ mile north of Big Cliff, Presidio Co., Texas.

Age.—Early Chadronian.

Material.—TMM 40206-4, LM^1; TMM 40203-49, LP^4-M^2; FMNH PM 83, RP_4-M_3; FMNH PM 133, RP_2-M_1. Of questionable reference are FMNH PM 106, L fragmentary dP^4 and M^{1-3}; FMNH PM 52, RP_4-M_2; and several isolated upper and lower teeth and astragali.

Diagnosis.—Upper molars with incomplete selenes, the postprotocrista meeting the prehypocrista at right angles much as in *Protoreodon.* In lower molars the metaconid is a distinct cusp but joined to the posterior internal crest by a ridge at right angles to the tooth.

Description.—Most of the upper teeth have the postprotocrista as described above. However, FMNH PM 106 has fully developed selenes on all molars. There is, therefore, likelihood that there was considerable variation in the Vieja population, if indeed it was a single population. I am assuming it was but emphasizing the primitive state of development of the upper molars and the distinct metaconid on P_4 by naming the new species. The lower molars are as in the other species of *Leptomeryx.* The skull is unknown.

TABLE 20.—MEASUREMENTS OF UPPER TEETH OF *LEPTOMERYX DEFORDI,* PORVENIR LOCAL FAUNA

	TYPE FMNH PM 58	TMM 40203-49	FMNH PM 106
M^1-M^3	17.9	–	18.2
P^4L	4.5	4.5	–
W	5.6	5.7	–
M^1L	5.9	6.2	5.7
W	6.5	6.8	6.0
M^2L	6.5	6.5	6.1
W	7.3	7.6	6.6@
M^3L	6.4	–	6.7
W	7.1	–	7.5

TABLE 21.—MEASUREMENTS OF LOWER TEETH OF *LEPTOMERYX DEFORDI*, PORVENIR LOCAL FAUNA

	FMNH PM 133	FMNH PM 83	FMNH PM 52	TMM 40202-3
P_2-P_4	15.1	–	–	–
M_1-M_3	–	21.4	–	–
P_2L	4.8	–	–	–
W	2.0	–	–	–
P_3L	5.3	–	–	–
W	2.6	–	–	–
P_4L	5.5	5.8	5.8	5.4
W	3.2	3.2	3.2	3.3
M_1L	–	5.7	6.3	6.2
W	–	4.0	4.2	4.3
M_2L	–	6.4	6.4	6.8
W	–	4.8	4.7	4.5
M_3L	–	9.4	–	–
W	–	4.7	–	–

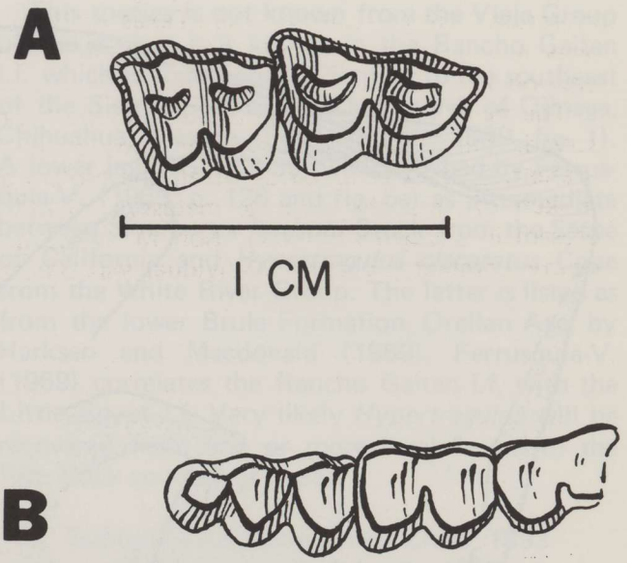


Figure 36.—*Hypisodus* cf. *minimus*, 40504-287. *A.* LM$^{2-3}$. occlusal view. *B.* Fragmentary RM$_1$, M$_{2-3}$, occlusal view. Airstrip l.f., Capote Mt. Tuff.

TABLE 22.—MEASUREMENTS OF UPPER AND LOWER TEETH OF *HYPISODUS*. FROM AIRSTRIP LOCAL FAUNA (40504) TEXAS, SOUTH DAKOTA, AND WYOMING

	40504-287	BRULE 40045		40504-287	40504-158	40283-6	ORIN JCT. WYO. 40518-3	DOUGLAS WYO. 40054
M^{1-3}		13.5	M_{1-3}					15.3
M^{2-3}	11.1	10.5						
M^1 L		4.3	M_1 L		4.3	3.9		3.6
M^1 W		4.6	M_1 W	2.9		2.9		2.6
M^2 L	5.4	5.2	M_2 L	4.5	4.8	4.7	4.1	4.2
M^2 W		4.8	M_2 W			3.4	2.7	3.0
M^3 L	6.4	6.1	M_3 L	6.9	7.2			6.5
M^3 W		5.0	M_3 W					2.6

Subfamily Hypisodontinae Cope, 1877
Genus *Hypisodus* Cope, 1873
Hypisodus minimus Cope, 1873
Hypisodus cf. *minimus*
Airstrip and Ash Spring local faunas
Figs. 35, 36; Table 22

Type.—AMNH 6543, upper jaw fragment with M$^{1-3}$.

Material.—Partial skull and jaw with left M$^{2-3}$ and right M$_{1-3}$, 40504-287; right jaw with P$_4$-M$_3$, 40504-158; right maxilla with partial P^4 and M$^{1-3}$, 40283-7; partial right ramus with M$_{1-2}$, 40283-6; and partial right M$_3$, 40283-106.

Stratigraphic position.—Specimens from locality 40504 are from the Capote Mt. Tuff, approximately 570 feet above the base and belong with the Airstrip l.f. Specimens from locality 40283 are from undifferentiated Vieja Group, approximately 105 feet below the upper ignimbrite (Tg6, table 2, of Wilson *et al.*, 1968) and approximately 510 feet above the Pantera Ignimbrite; Ash Spring l.f., the highest stratigraphically in the Vieja Group.

Age.—Chadronian.

Description.—The specimens of *Hypisodus* from west Texas are not well preserved. Those from the Airstrip l.f., 40504-287 (fig. 35) and –158 are the earliest occurrences that I know of. In M$^{2-3}$ of 40504-287 (fig. 36), the lobes are still prominent, but the enamel does not extend below the level of the maxilla on the external margin of the alveoli. In other words, the teeth are not as high-crowned as the Brule specimens described by earlier authors (Scott, 1940; Troxell, 1920). The styles on M^3 are not as prominent. Although the sample is very small, the measurements of the teeth from the

Chadronian are larger than any given in the literature. Unfortunately, the Texas collection does not have specimens in which premolars are preserved.

The maxillary fragment, 40283-7, is poorly preserved; only the most posterior root of P^4 is present. The external cusps of all the molars are broken off, but the elongate metastyle of M^3 is present in a fragmentary condition. M^1 is the most nearly complete, but the individual was old and the occlusal pattern worn off. The protocones on M^2 and M^3 have a posterointernal extension which squares their internal edges. The proto- and hyposelenes on M^1 and M^2 are closer together but separated in M^3 as described by Troxell (1920).

The lower molars are hypsodont. The crown pattern on M^1 and M^2 is worn in 40283-6. The M^3 in 40203-106 is less worn and has three roots that are joined similarly to those found in *Hypisodus* from the Brule Fm. of the middle Oligocene of Douglas, Wyoming.

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